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ANATOMICAL AND PHYSIOLOGICAL STUDIES OF KNEE JOINT INNERVATION IN THE CAT

By

STEN SKOGLUND

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Ivar Hæggströms Boktryckeri AB

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Preface

Professor Bror Rexed originally interested me in the problems of joint innervation. His invaluable support, able criticism and unfailing interest have meant everything for carrying through this work.

For initiating me into neurophysiological work and for his continuing guidance in it I express my great indebtedness to Professor Ragnar Granit. In the stimulating atmosphere of his laboratory, I found opportunities for informal discussions with colleagues to whom I owe more than can be acknowledged individually.

I am grateful to Dr. Charles Phillips, Fellow of Trinity College, Oxford, for his kindness in reading the manuscript.

My thanks are also due to Dr. Björn Lindahl for the drawings, and the Technical Staffs of both Institutes for their assistance.

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Uppsala, February 1956.

STEN SKOGLUND

General Introduction

Physiologists have long taken an interest in how information about position and movement of a limb arises in the periphery and is perceived. SHERRINGTON, in a textbook article in 1900, pointed out that "muscle sense" means recognition of position, of active and passive movement and of resistance to movement. These sensations must, he considered, arise in muscles, joints and bones. During the last 50 years anatomical and neurophysiological research have produced an ever increasing knowledge of the innervation of muscle while the knowledge of joint proprioception has advanced less rapidly.

Some points concerning the innervation of muscles are of interest in connection with the present investigation. The largest afferent fibres in a muscle nerve, the so-called Group I fibres which conduct impulses from the annulo-spiral endings and the Golgi tendon organs have been shown by LLOYD and MCINTYRE (1950) to ascend for a short distance only in the dorsal funiculi, and not to take part in forelimb—hindlimb reflexes (LLOYD and MCINTYRE 1948). Nor do their impulses reach the sensory areas of the cerebral cortex (MOUNTCASTLE, COVIAN and HARRISON 1952). On the other hand the Group II fibres of the muscle nerves which are connected to the flower-spray endings (MATTHEWS 1933, for discussion see GRANIT 1955) take part in the forelimb-hindlimb reflexes according to LLOYD and MCINTYRE (1948). Contrary to MOUNTCASTLE et al. (1952) MCINTYRE (1953) states, that these fibres are represented in the cerebral cortex. These authors agree that there is a constant representation in the cortex of Group III fibres of muscle nerves.

The investigations just mentioned indicate that muscle proprioception is represented in the cerebral cortex only through impulses from the flower-spray endings and the sensory endings connected to Group III fibres. GRANIT in his Silliman Lectures

"Receptors and Sensory Perception" (1955) does not use the term "muscle sense" because he considers it premature to venture beyond general statements as long as we lack detailed information about the innervation of joints.

The present work deals with impulse patterns from joint receptors mediated by myelinated nerve fibres. It is a study of the anatomy and physiology of knee joint innervation in the cat.

Relatively few studies have been made of the distribution of articular nerves in animals. The nerves to the knee joint in the mouse and the cat were mapped out by GARDNER (1942 and 1944).

Termination of articular nerve fibres has been the subject of several studies, both in man and animals, but the findings of different authors are by no means in agreement. Textbooks of histology, for instance the one by MAXIMOV and BLOOM (1952), state that Vater-Pacini corpuscles are always present in joints. These endings were described by RAUBER in various joints (1867). KRAUSE (1874 a, b), on the other hand, found them not to be real pacinian corpuscles whereas RAUBER (1874) argued that they were of a similar nature and called them modified Vater-Pacini corpuscles. KRAUSE later (1881) found various types of endings which he termed end bulbs. GERLACH (1889) described both pacinian corpuscles and KRAUSE end bulbs in the joint capsule. SFAMENI (1902) described endings which were similar to those described by RUFFINI (1894) in the skin. This type of ending had earlier been discovered by NICOLADONI (1873). SFAMENI found no Vater-Pacini corpuscles in joints. [For a complete historical review the reader is referred to SAMUEL (1948) and GARDNER (1950 a).]

GARDNER (1944) studied the knee joint innervation in the cat. He described endings in the joint which were similar to the ones found by RUFFINI in the skin, and stated that there were no pacinian corpuscles in or near the joint. In addition GARDNER gave a description of how the knee joint receives its innervation and made measurements of the nerve fibre diameters of some of the nerves supplying it. His findings are on some points in disagreement with those of other authors (to be mentioned below)

and some of his results are based on too small a number of animals.

In a series of papers GARDNER (1948, 1950 b) and GARDNER and coworkers (1949, 1952, 1953) have studied the dorsal root inflow of afferent fibres from the knee joint of the cat, the reflex effects of these fibres and their central connections. For reasons to be dealt with in detail under the various headings of this thesis the results of GARDNER and GARDNER et al. in these papers have only in part been accepted.

BOYD (1953 a) and BOYD and ROBERTS (1953) described slowly adapting endings in the posterior part of the knee joint capsule in the cat and attributed to these endings the ability to signal position and movement. These authors also described rapidly adapting endings in the posterior part of the joint capsule but they did not analyse this response.

ANDREW and DODT (1953) studied sensory endings in the anterior part of the knee joint capsule in the cat and found slowly adapting endings which they thought could signal position and movement. They did not investigate these endings in detail, but restricted their study mainly to endings which they claimed were able to signal the tension of the medial collateral ligament in which ANDREW (1954) found Golgi endings. BOYD (1953 b and 1954) found that the slowly adapting response in the posterior part of the joint emanated from Ruffini endings and the rapidly adapting response from modified pacinian corpuscles.

None of the authors mentioned above has made a complete study of knee joint innervation in the cat and their findings are on several points in disagreement. Some results also stand in need of confirmation. The present work is designed as a fairly extensive survey. The following specific problems have been treated:

1. What is the nature and definition of the stimuli that the joint receptors respond to?

2. How does the response to such stimuli relate to a number of factors such as a) anatomy and location of receptors, b) fibre size, c) accessory forces such as stretch and contraction of muscles attached to the joint?

3. Does the afferent inflow from the joint activate flexor and extensor limbreflexes?

4. Does it project to the cerebral cortex?

Answers to these questions should throw light on the way in which the various joint receptors combine to make it possible to discriminate between different positions, and to signal the direction and velocity of movements, and the degree of resistance these movements may encounter.

CHAPTER I

Distribution, termination and calibre spectra of nerves to the knee joint

SASAOKA, in 1939, first systematically investigated the articular nerves in the cat. He found only one branch to the knee joint coming from the tibial nerve. On this he also made diameter measurements of the fibres. GARDNER (1944) studied the distribution and termination of nerves in the knee joint of the cat in both adult animals and foetuses. He stated that the joint is innervated by nerves running directly to it as well as via the muscles. He measured the nerve fibre calibre spectra in only four of each of the two nerves which run directly to the knee joint. GARDNER could only find one type of ending in the joint capsule, namely the Ruffini ending. On the other hand SAMUEL (1948, 1949 and 1952) described various other kinds of endings. BOYD (1953 b and 1954) found both Ruffini endings and a sort of modified Vater-Pacini corpuscles in the posterior part of the joint capsule. Also in disagreement with GARDNER's results is ANDREW's finding of Golgi tendon organs in the medial collateral ligament (ANDREW 1954).

GARDNER's study is the only one dealing with all aspects of the anatomy of the knee joint innervation in the cat. However, some of his results are based on too small a number of animals and in some respects differ widely from the findings of other authors. Before studying the physiology of the joint receptors, the anatomy of these receptors and their nerves must be re-examined, and the discrepancies between the findings of the various authors must be settled in one way or another.

The questions of interest for a physiological study of joint innervation are: what courses do the nerves take to the joint? What kind of myelinated fibres do they contain? How are the fibres distributed in the joint? What types of endings do they form, and what fibre sizes are these endings connected with?

METHODS

Macroscopic dissection. The joint nerves of the knee have been dissected in 15 adult cats. The leg was first macerated in 1 % acetic acid for 48 hours and then washed in running tap water. This procedure makes the muscles easily dissected. The dissection has been carried out under water with the aid of a dissecting microscope.

Electrophysiological method. In 50 cats used also for other purposes in this work the obturator and femoral nerves have been electrically stimulated and action potentials led off from that nerve which together with the genu suprema branch of the femoral artery runs to the knee joint.

Histological methods. 30 medial nerves and 30 posterior nerves (see below) were impregnated with osmic acid for 24 hours and cut in 10 micron sections. Good sections from this material were selected for photography in a magnification of 1000x. Measurements of nerve fibre diameters were then made from paper copies according to the method used by REXED (1944).

In 4 animals the sartorius muscle was removed together with the joint capsule surrounding the insertion of its tendon. These specimens were sectioned serially at 15 microns and stained according to the modified ALZHEIMER-MANN-HÄGGQUIST method (REXED 1948). This method applied on cross-sections of muscles is far from the best for tracing nerve fibres over long distances and to work out the whole supply of joint nerves running via muscles. It has, however, been used because it is one of the few methods that can give an answer to the question of what fibre sizes are represented in the articular branches taking their course through muscles.

In 5 cats the joint capsule was removed together with the entry of the articular nerves, fixed in BOUIN's solution for 48 hours, cut in 15 micron sections and stained according to the silver method of PALMGREN (1948). In 15 cats the joint capsule, the medial collateral ligament and the cruciate ligaments were removed, stained according to the gold chloride method of LOEVIT (ROMEIS 1948) and teased. In these preparations the nerve endings are beautifully stained, and the diameter of the fibres to the sensory endings can be measured. Such gold stained and teased material is not, however, well suited for photography, on account of the thickness of the tissues, and it has been necessary to superimpose several exposures at different depth of focus to get good pictures. The measurements of nerve fibre diameter in this material is difficult because of the faint staining of the myelin sheath. Though exact values are not obtainable in this way, the method can be used for a rough estimation of fibre size. The procedure has been to measure the fibre at several points over a considerable length using a micrometer scale in the eyepiece of the microscope. Thus no errors of photography have been introduced here and distortion in the preparation could to some extent be controlled.

RESULTS

Distribution of nerves to the knee joint

Macroscopic dissection. From the tibial nerve in the popliteal fossa there arises a slender nerve twig which as a rule is the first branch of the tibial nerve. This nerve twig runs a recurrent course through the popliteal fat to the posterior part of the joint capsule (Fig. 1). Sometimes it divides into two branches on its way. In two cases it has not been possible to find the nerve. Possibly the division of the nerve was so high that the small branches could not be recognized with the technique used. GARDNER (1944) called this branch the *posterior* nerve and that name will be used throughout this work. No other branch of the tibial nerve than

Fig. 1. Schematic drawing showing the course of the posterior nerve to the posterior part of the knee joint.

the one described has been seen to take part in the innervation of the knee joint.

Out of the peroneal nerve, as it winds round the fibula, come one or two small filaments that innervate the lateral side of the posterior part of the joint. In 1 animal two branches of the peroneal nerve were seen to enter the joint capsule. In 4 of the animals no contribution of the peroneal nerve to the innervation of the joint capsule could be detected.

One or two slender nerves that enter the knee joint capsule on its medial side (Fig. 2) run together with the genu suprema

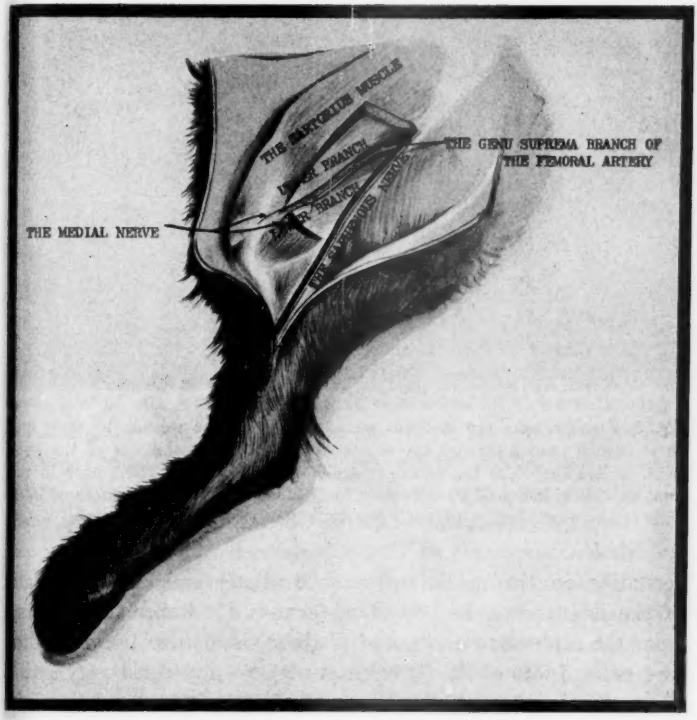


Fig. 2. Schematic drawing showing the course of the medial nerve, in this case divided in two branches.

branch of the femoral artery underneath the sartorius muscle. This nerve has been called the *medial* one by GARDNER (1944), a name which will be used throughout this work. Macroscopic dissection has revealed, that the medial nerve as a rule comes from the saphenous nerve. When there are two filaments one on each side of the genu suprema artery, the lower branch comes from the obturator nerve. In one case both branches arose from the femoral nerve. When there is only one branch, this always divides in two when it approaches the joint.

Stimulating the obturator or saphenous nerve electrically and

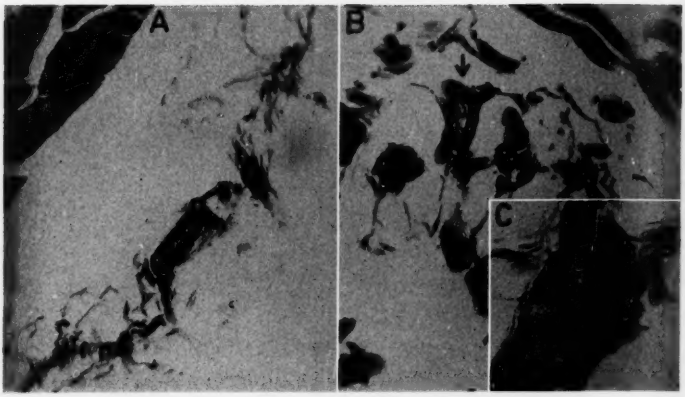


Fig. 3. Sections from the sartorius muscle and the joint capsule to show one nerve branch passing through the muscle to the medial ventral side of the knee joint. A. The branch in the muscle (magnification 168 ×). B. The branch in the joint capsule as indicated by the arrow (magnification 372 ×). C. The same as B with higher magnification (975 ×) ALZHEIMER-MANN-HÄGGQUIST stain.

recording on the medial nerve, immediately reveals the origin of the joint nerve. In 26 out of 50 cats the entire nerve came from the saphenous nerve, and of these there were two branches in 8 cases. In 10 of the 50 animals with an undivided nerve, this derived from both the saphenous and obturator nerves and in these cases technical difficulties made it impossible to decide whether or not the two end branches of the medial nerve contained fibres from both nerves. In 12 others of the 50 cats the medial nerve was divided in two branches, the lower one of which came from the obturator nerve, and the upper one from the saphenous. An undivided nerve was in 2 cases derived entirely from the obturator nerve.

In 12 of the 15 animals used for macroscopic dissection a nerve branch was found running between the rectus femoris and vastus intermedius together with some vessels. This nerve seemed to be directed exclusively to the joint.

In the sartorius muscles stained according to the modified ALZHEIMER-MANN-HÄGGQVIST method, it was possible to trace

nerve fibres, that went through the muscle down into its tendon. In one of the specimens the nerve could be followed into the joint capsule (Fig. 3). In the others nerve branches were traced well down into the tendon, but they could not with certainty be followed into the joint capsule on account of their deviation in course. Amongst the fibres traced into the capsule there were some which reached a diameter of 12—13 microns, without correction for the shrinkage of the fibres.

Calibre spectra of joint nerves

Of the 60 nerves stained with osmium for measurements of fibre diameter, only 18 posterior and 22 medial nerves could be used. The others were either poorly stained or it was not possible to get a good cross-section. Of the nerves fit for use the posterior nerve averaged 176 myelinated fibres and the medial 145. It soon became apparent that the nerves differed widely in number of fibres from animal to animal, so that comparisons between the two nerves seemed to be valuable only in the same animals.

Of the well-stained nerves 10 happened to be pairs, and Table I and II give the fibre diameters of the posterior and medial nerves in these cases. From the tables it can be seen that the number of fibres in the medial nerve varied from 61 to 296 and in the posterior from 53 to 249. As an explanation of these wide variations might be suggested, that in the medial nerve one of the branches had been missed and that in the posterior nerve the division of the nerve had been so high that one branch had been overlooked. Such sources of variation can of course never be excluded. Another equally possible explanation is that the nerve supply through muscles and from the peroneal nerve is more abundant in the cases in which the posterior and medial nerves are small.

In Table I it is seen that nerves 8, 9 and 10 have two branches, (the upper U and the lower L), and that there is no difference between their calibre spectra. Of the other 12 medial nerves not presented in Table I, 5 had two branches, and no difference was found between their fibre diameters either.

Table I. The calibre spectrum of the medial nerve.

Animal No.	1— 2 μ	2— 3 μ	3— 4 μ	4— 5 μ	5— 6 μ	6— 7 μ	7— 8 μ	8— 9 μ	9— 10 μ	10— 11 μ	11— 12 μ	12— 13 μ	13— 14 μ	14— 15 μ	15— 16 μ	16— 17 μ	17— 18 μ	Sum	Total sum
1.	4	31	28	13	19	21	13	13	10	10	7	4	1	1				175	175
2.	7	11	3	1	9	4	8	7	1	3	4	2	1					61	61
3.	1	40	23	11	11	9	6	7	14	8	7	8	11	1	6	3	1	167	167
4.	1	24	14	8	7	11	3	2	4	2								76	76
5.		10	1	23	25	27	16	10	7	2	7	4	1					133	133
6.		10	29	36	29	16	17	14	26	33	34	26	14	7	1	4		296	296
7.	1	10	21	12	12	14	5	12	8	7	4	6	1	3	5	3		124	124
8 U.		17	11	7	8	7	6	5	8	6	9	2						86	131
8 L.		4	9	4	9	6	4	3	1	1	3	1						45	
9 U.				4	7	6	8	6	4		3							38	160
9 L.		17	30	18	13	10	12	6	7	5	2	1	1					122	
10 U.	14	31	35	24	6	4	2	4	2	1	1							124	261
10 L.	8	11	16	21	21	17	16	7	8	4	7	1						137	

Table II. The calibre spectrum of the posterior nerve.

Animal No.	1—2 μ	2—3 μ	3—4 μ	4—5 μ	5—6 μ	6—7 μ	7—8 μ	8—9 μ	9—10 μ	10—11 μ	11—12 μ	12—13 μ	13—14 μ	14—15 μ	15—16 μ	16—17 μ	17—18 μ	Sum	Total sum
1.	1	9	19	20	17	19	10	7	7	9	4	2	3	1	1			129	129
2.		5	8	17	12	7	6	6	3	3								67	67
3.	3	12	23	23	23	14	17	16	16	11	13	9	5	3	2	1	1	192	192
4.	3	7	10	4	5	9	1	3	3	4	3	1						53	53
5.	15	23	11	12	16	13	7	4	2	2								105	105
6.	6	20	12	12	11	2	3	1		1								68	68
7 B.	1	14	12	4	11	14	16	20	17	13	3	1						126	164
7 S.		9	10	1	5	1	1	1	1	1	1	3	2	1	1			38	
8 B.	2	12	17	3	10	22	18	30	18	9	7	5						153	249
8 S.	3	11	13	13	12	13	11	8	1		1	4	2	3	1			96	
9 B.	1	13	16	16	12	13	19	10	10	2	2							114	198
9 S.	1	7	10	15	13	16	7	4	1			2	5	2	1			84	
10 B.	2	14	18	20	13	17	12	15	7	2								120	201
10 S.		6	14	14	14	9	3	2	4	1		1	3	6	3	1		81	

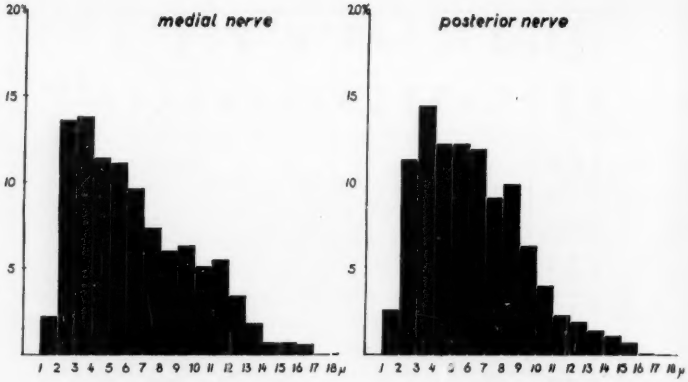


Fig. 4. Diagrams showing the distribution of different fibre sizes in the medial and posterior nerve to the knee joint in the cat, plotted against percentage of total number of fibres in ten nerves of each.

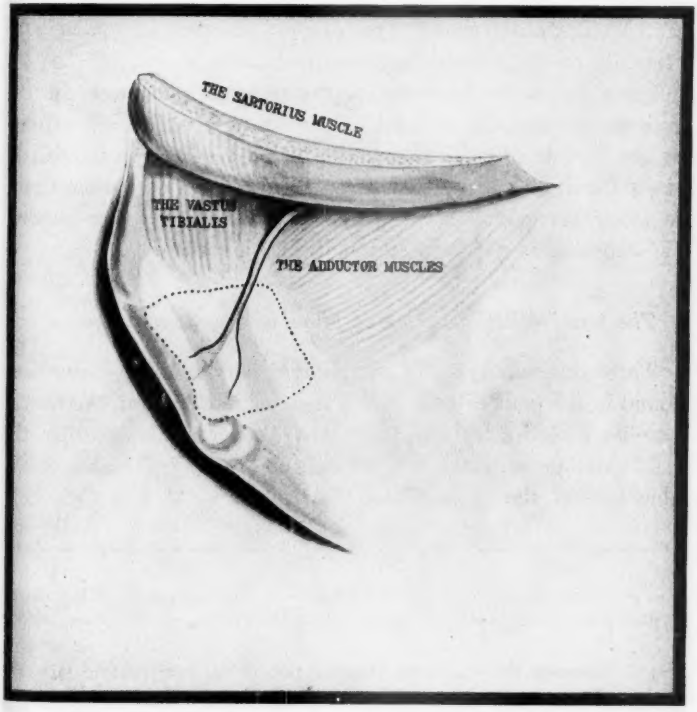
In Table II the numbers 7, 8, 9 and 10 are seen to have two branches, one big (B) and one small (S). These branches seem to differ in the following way: the big branch contains no fibres with a diameter over 12—13 microns but many in the range from 10—12 microns, the small branch has rather many fibres over 12 microns but very few fibres in the range from 10—12 microns. In two of the 8 posterior nerves, having two branches (not presented in Table II), this was also found to be the case.

Drawing a graph of the different fibre diameters and plotting them against percentage of total number of fibres will give a picture of the relationship between different fibre diameters. The graphs in Fig. 4 of the 10 pairs of nerves show the medial and the posterior nerves to have more or less the same fibre distribution. The wide variations seen in the macrodissection in the nerve supply to the knee joint do not allow further conclusions.

Fig. 5. Schematic drawing of the medial ventral side of the knee joint to show the main area (within dotted line) of the distribution of fibres connected to the medial nerve.

The distribution of nerves within the joint capsule

In sections, stained according to the silver method of PALMGREN, the distribution of nerve fibres within the capsule can be worked out. In the ventral part of the joint capsule most of the fibres from the medial nerve are distributed within the area outlined in Fig. 5. Soon after the entrance of the medial nerve in the capsule one branch (the upper) continues towards the patellar ligament and divides into small branches on its way; the lower one bends off more caudally. The main part of the nerve fibres are seen to lie in the superficial part of the capsule



(Fig. 6). Round the medial collateral ligament dense bundles of nerve fibres run in a craniocaudal direction. With the method used it has not been possible to decide if the innervation of the cruciate ligaments derives from the medial nerve. Nor has it been possible to work out the exact region of distribution for either the upper or the lower branch of the medial nerve, on account of the contribution of nerve fibres from other sources, but they seem to overlap to some extent.

In the posterior part of the joint capsule the fibres of the posterior nerve innervate the area outlined in Fig. 7. In this part of the joint capsule the nerves also run very superficially. One small branch of the posterior nerve is always seen to pierce the capsule (Fig. 8). This branch may take part in the innervation of the cruciate ligaments. This cannot, however, be stated with certainty on the evidence of these preparations.

From the nerve branches in the outer fibrous layer of the capsule are seen fibres taking their course to the deeper parts of the capsule often accompanying blood vessels. On account of the difficulty to distinguish fine nerve fibres from other tissue in silver stained material the innervation of the inner part of the capsule has not been systematically investigated.

The termination of the nerve fibres in capsule and ligaments

Three different types of complicated nerve endings have been found in the joint capsule and in the medial collateral, the medial patellar and the cruciate ligaments. As pointed out earlier the gold chloride technique is a difficult one to apply because of the thickness of the capsule and the ligaments. At any rate, gold

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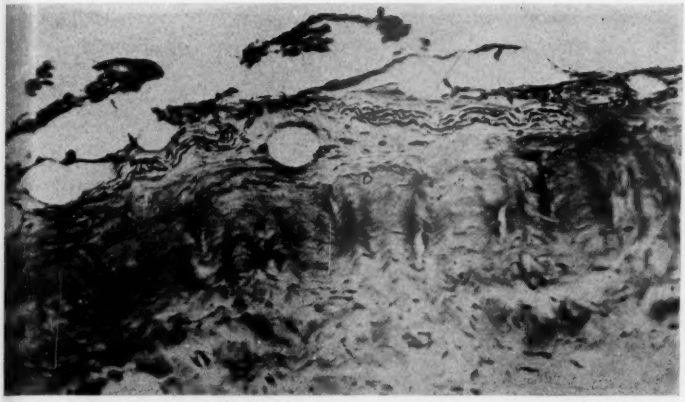
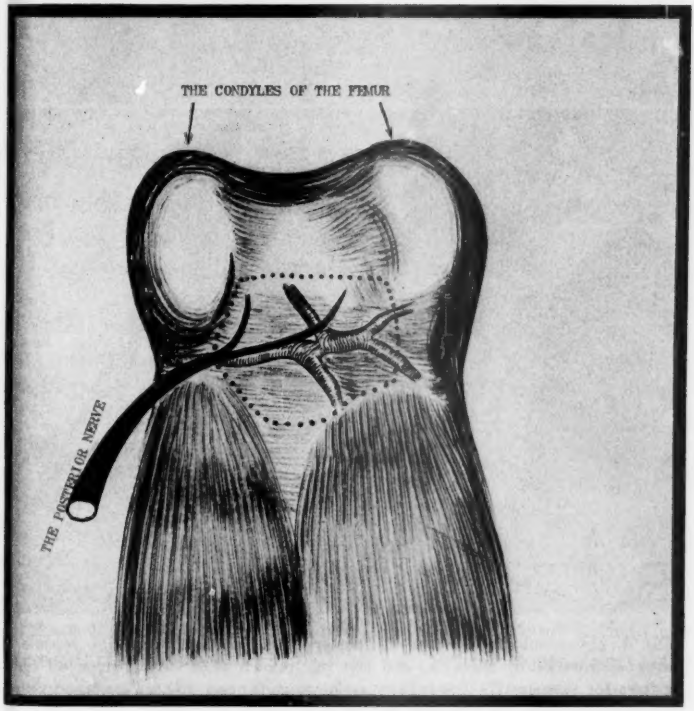
Fig. 6. Picture to show the superficial course of the nerve fibres in the medial ventral side of the knee joint capsule (PALMGREN stain, magnification 132 ×).

Fig. 7. Schematic drawing of the posterior part of the knee joint to show the main area (within dotted line) of distribution of fibres from the posterior nerve.

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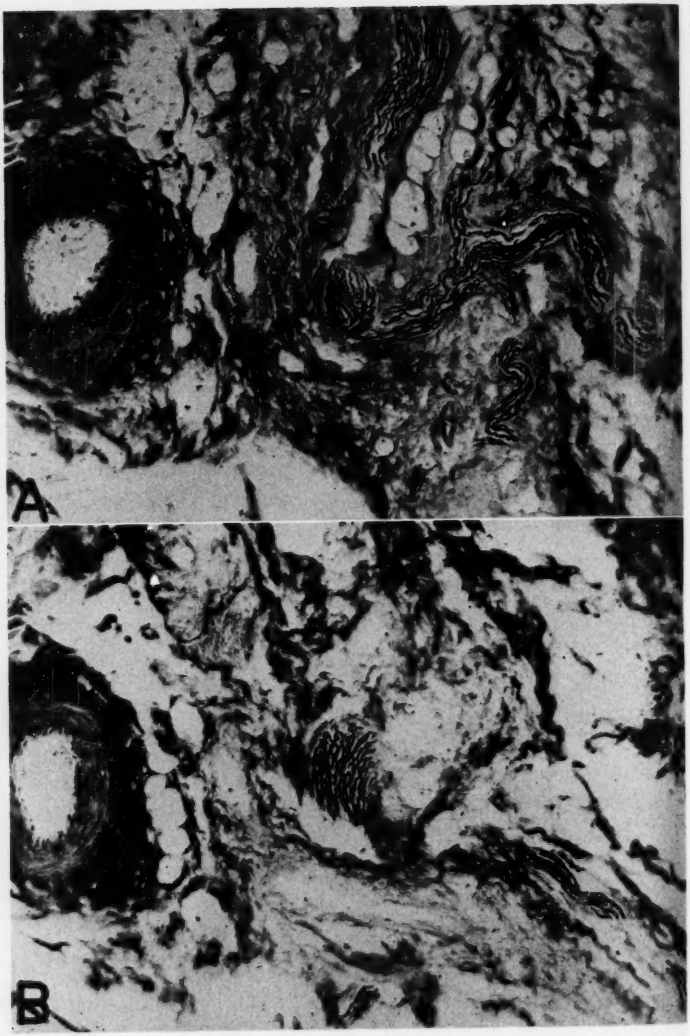

Fig. 8. Microphotographs from the posterior part of the knee joint capsule to show distribution of fibres (A) and how one branch after having given off fibres pierces the capsule (B). PALMGREN stain, magnification 130 ×.

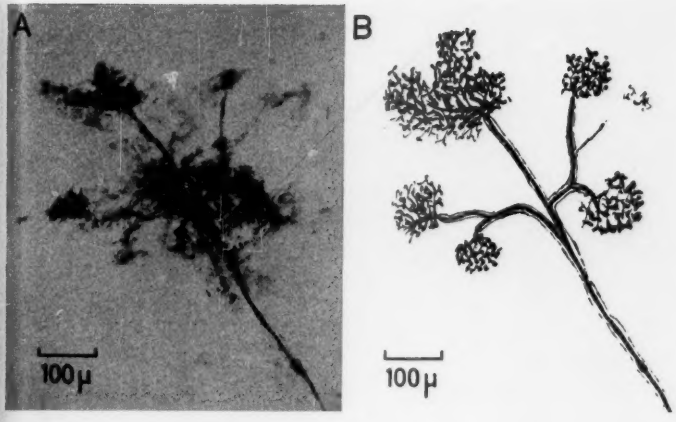

Fig. 9. A sensory unit of the Ruffini type in the posterior part of the joint capsule. Five endings arising from the same axon. A. Microphotograph (magnification 132 ×). Gold stain. B. A drawing of the endings seen in A at the same magnification. (The drawing is a combination of a camera lucida picture, with details added freehand after further microscopic examination.)

chloride is a better stain for this purpose than silver impregnation which has also been tried.

The type of ending found within the areas of the joint capsule outlined in Figs. 5 and 7 may appear in groups up to five arising from one axon (Fig. 9). Sometimes a single ending occurs. The axon loses its myelin sheath shortly before it enters the sensory ending and then continues into the ending proper where it divides into a network of very fine fibres surrounded by a faintly stained capsule. These endings are very similar to those described by RUFFINI (1894) in the skin. They are in the following called Ruffini endings, a name which was first suggested for them by SFAMENI (1902). The Ruffini endings are now and then seen to be accompanied by one or two accessory fibres which run together with the primary axon into the ending.

As mentioned above the Ruffini endings are found both in the ventral and the posterior part of the joint capsule. They also occur occasionally in the medial collateral ligament or in its

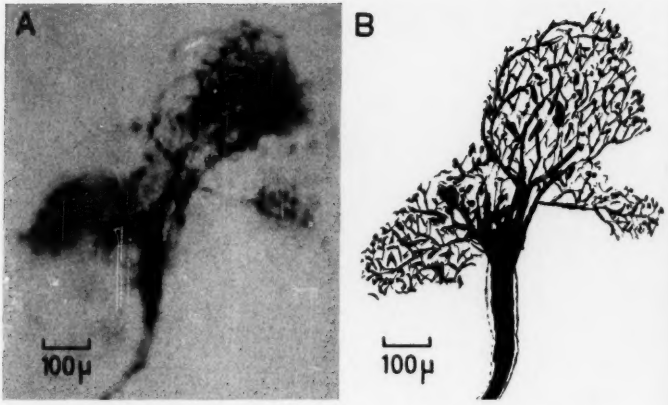

Fig. 10. Golgi ending in the anterior cruciate ligament. A. Microphotograph (magnification 110 ×). Gold stain. B. Drawing of the ending seen in A at the same magnification. (The drawing is made in the same way as in Fig. 9.)

vicinity, but never in the cruciate ligaments. They always lie in the outer fibrous part of the capsule and there is no obvious difference in number of them in the ventral and posterior part of the capsule.

On the surface of the cruciate ligaments as well as in the medial collateral ligament and the medial patellar ligament is found a type of nonencapsulated ending (Fig. 10) which is very similar to the ones found in the musculo-tendinous junction, the so-called Golgi tendon organs. These endings never lie in the capsule proper. The Golgi endings are fewer than the Ruffini endings. Their axon divides dichotomously several times and then ends in a fine network. The Golgi endings, as seen in the figure, are very much bigger than the Ruffini endings.

The third type of sensory ending in the joint is very infrequent, and in each preparation only two to three have been found in the posterior part of the joint capsule and one to two in the anterior. These endings are a kind of modified Vater-Pacini corpuscle. The axon is seen to enter a cone-shaped body con-

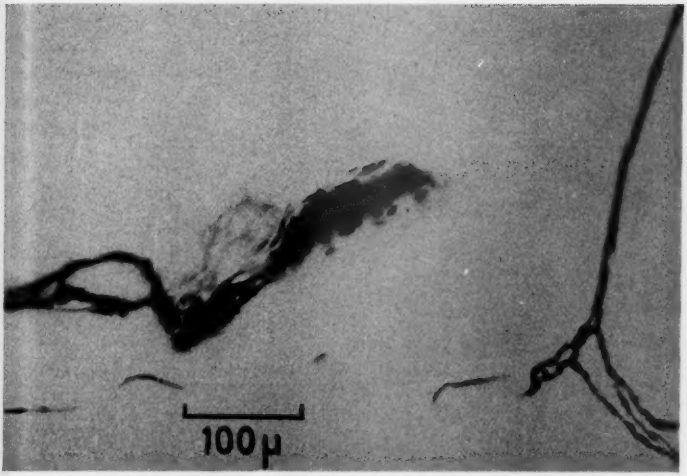

Fig. 11. Modified Vater-Pacini corpuscle in the capsule. Magnification 185 ×. Gold stain.

sisting of layers never exceeding 20 in number. In this bulb the axon ends with a little knob (Fig. 11).

No other types of complicated sensory endings than those described above have been found in the joint capsule or in the ligaments but many free nerve endings are present. Various kinds of coiled nerve branches and clubshaped fibres have been seen, but careful examination has revealed them to be artefacts of this teased material or due to the stain being too heavy.

The difference in size between the Ruffini endings and the Golgi endings seems also to be reflected in the size of their nerve fibres. Measurements of fibre diameter on teased gold stained material cannot, of course, give exact values, but it can be used for a rough estimation. In the table below the first figure given is the lowest value measured, the second the difference from the highest.

In 20 Golgi endings measured the lowest value of axon diameter was 9 microns and in 50 Ruffini endings the lowest value was

Table III.

	Axon diameter in microns (lowest value)	Difference in microns from highest value
Preparation I		
Ruffini ending	6	1
" "	8	2
" "	7	3
" "	5	2
Golgi ending	10	2
" "	12	1
" "	14	1
Preparation II		
Ruffini ending	7	3
" "	5	3
" "	8	1
" "	5	2
" "	9	1
" "	8	2
Golgi ending	9	1
" "	13	1
" "	11	2

5 microns. The highest value in the first case was 15 microns and in the latter 10 microns.

The diameter of the axon connected with the modified Vater-Pacini corpuscles has been measured in 7 preparations only. It never exceeded 13 microns.

DISCUSSION

From this work as well as GARDNER's (1944) it can be concluded that in the cat the nerve supply to the knee joint is quite variable. The existence of two nerves, a medial and a posterior one, should, however, be regarded as well established (GARDNER 1944;

SAMUEL 1948; ANDREW and DODT 1953, and BOYD and ROBERTS 1953). The statement of ANDREW and DODT (1953), that the medial nerve in about half the cases is divided in two branches, has been confirmed in a considerable number of animals.

This investigation confirms the finding of GARDNER, that in the cat the knee joint receives part of its nerve supply through the muscles (see also SAMUEL 1948). GARDNER's technique, making use of foetuses, is much better for this demonstration than the macrodissection used in this work. The fact that part of the nerve supply of the joints is from muscle nerves, is of great importance in animal experiments as an unknown number of articular fibres will be intermingled with the afferent muscular fibres proper. This is the case not only in the cat, but also, as shown unequivocally by WRETE (1949), in the shoulder joint of man. To judge from the investigations of RÜDINGER (1857) it may be the general principle in the innervation of the joints of the human body.

This investigation shows three types of complicated endings in the joint, with the Golgi ending only in the ligaments and the Ruffini ending and modified Vater-Pacini corpuscle in the capsule. These results complete the observations of SAMUEL (1948, 1949 and 1952); of BOYD (1954), who observed two types of receptors in the joint capsule; of ANDREW (1954), who reported that the medial collateral ligament is equipped with Golgi organs but was unable to find them in other places, and of BOYD (1954), who on one occasion observed a Golgi ending in one of the cruciate ligaments. GARDNER also described Ruffini-like endings in the joint capsule. He worked with silver stained and sectioned material, which might explain why he found so few endings and why he was not able to see the endings in the ligaments.

In the silver stained material used in this work, it was not possible to determine exactly the distribution of the nerve fibres within the joint but they were mainly distributed to the capsule and the ligaments. In the case of the medial nerve it was found that the lower and upper branches to some extent overlapped. In the areas of distribution of these nerves there is a contribution of fibres from other sources which confuses the picture.

Neither the silver nor the gold method used has been found

suitable for studying the innervation of the periosteum or cartilage within the joint. In gold stained preparations nerve fibres were seen in the menisci but no endings. According to SFAMENI (1902) the menisci in the knee joint of the dog are supplied with many free nerve endings and some kind of "plaquette nerveuse". From his description as well as his pictures the last mentioned ones appear to be a kind of free nerve endings too. The periosteum on the other hand should according to SFAMENI be equipped with Ruffini endings. On the basis of the findings in the silver stained material, that most of the fibres from the direct articular nerves are distributed to the capsule and the ligaments, it can be stated that the endings in the menisci and periosteum connected to these nerves are few. They are therefore not considered in the physiological analysis of the joint receptors which exclusively is done on the direct nerves.

A rough estimation is presented in this work of the size of nerve fibres connected to the different types of sensory endings. Taking the highest values measured, the Ruffini endings are connected to fibres between 7—10 microns and the Golgi endings to fibres between 10—15 microns. There is some evidence for this in the calibre spectra of the articular nerves. The group between 7—10 microns is very much larger than the one between 10—15 microns. This corresponds to the more frequent occurrence of the Ruffini endings as compared with the Golgi endings. The few modified Vater-Pacini corpuscles may also, as the measurements suggest, fall in the latter group. That the endings are supplied by fibres with different diameters tallies with the difference in their size.

In the calibre spectra of the posterior nerve there is another feature which in this connection is of some interest. In the posterior nerves with two branches, the small one contains all the large fibres but very few in the group which should be connected to Ruffini endings. The posterior nerve divides in two branches either on its way from the tibial nerve or when the nerve has reached the capsule. In the silver stained material one branch was always seen to pierce the capsule, but with the method used it could not be demonstrated with certainty, that it passed to

the cruciate ligaments. Probably the small branch seen in Table II is the same as the one piercing the capsule, the reason for this being that it contains fibres of exactly the right size for the Golgi endings in the cruciate ligaments. Thus many observations point to the conclusion that the different types of sensory endings are connected to nerve fibres of different size.

The conclusion drawn above immediately leads to the question of what function the numerous group of myelinated nerve fibres ranging from 2—7 microns may have. SAMUEL (1952) compared the innervation of joints in sympathectomised and normal animals and found that a large group of the myelinated fibres were of autonomic origin. It is also known that joint pain is very strong, and some of the fibres in the 2—7 micron group may well mediate pain of the so-called delta pain type (HEINBECKER, BISHOP and O'LEARY 1933; ZOTTERMAN 1939).

The nerve fascicles reaching the joint via the muscles contain fibres of the same size as do the posterior and medial nerves. The nerve fibres supplying specialised endings will then mainly fall in Group II but also in Group I. In this investigation the specimens stained with the ALZHEIMER-MANN-HÄGGQUIST method contained fibres which could be followed through the sartorius muscle well beyond the musculo-tendinous junction and some clearly into the joint capsule. As can be seen in Fig. 3 these myelinated fibres reach a diameter of Group I size. Thus it can be stated, that some muscle nerves receive an unknown number of fibres from the joints, some of which clearly contribute to Group I and II of the muscle nerves.

SUMMARY

1. The distribution, termination and calibre spectra of nerves to the knee joint of the cat have been studied with various techniques.

2. By macrodissection it has been observed that the knee joint receives its innervation partly from nerves running to the joint through muscles and partly by direct articular branches of the

obturator, saphenous, tibial, and peroneal nerves. Two of these branches are nearly always found, namely the one coming out of the saphenous and/or the obturator nerves, called the medial nerve, and the one coming out of the tibial nerve, called the posterior nerve.

3. Counts of the number of myelinated fibres in the medial and posterior nerves give very variable totals. Calibre measurements of the fibres in the medial and posterior nerves show them to contain myelinated fibres from 1 to 17—18 microns. The distribution of the different fibre sizes in the two nerves is more or less the same.

4. The distribution in the capsule of the fibres coming from the medial and the posterior nerves has been worked out in silver stained material. However in the areas of the capsule where these nerves ramify, there is a contribution of fibres from nerves running through muscles to the knee joint and of fibres from the peroneal nerve.

5. Three types of sensory end organs are found in various parts of the joint in gold stained material. In the medial collateral ligament, the medial patellar ligament and the cruciate ligaments, but never outside these structures, are found Golgi tendon organs. In the capsule are found Ruffini endings which are relatively more numerous than the Golgi endings. These are on the other hand very much larger than the Ruffini endings. In the capsule are also found a sort of modified Vater-Pacini corpuscles, very few in number.

6. Measurements on gold stained material of the diameter of nerve fibres supplying the different types of endings show the Golgi endings to be connected to fibres between 10—15 microns, while the Ruffini endings have fibres of 7—10 microns. This result tallies with the difference in size of these two types of endings. The different numbers are reflected in the calibre spectrum of the nerves. There is also some evidence that the cruciate ligaments get part of their nerve supply from the posterior nerve.

7. It is concluded that the nerves coming from the joint which run through the muscles add an unknown number of fibres to Group I and II of some muscle nerves.

CHAPTER II

The sensory discharge from the knee joint and its relation to the sensory nerve endings in capsule and ligaments

GARDNER (1948) in a study of the conduction velocity of joint nerves recorded action potentials in the posterior nerve. He observed a spontaneous discharge, the frequency of which could be altered by gentle pressure on the joint capsule with a glass rod. In 1953 (a) BOYD in a preliminary note described slowly adapting sensory endings connected to the posterior nerve. The same year ANDREW and DODT (1953) published their findings in the medial nerve. These two authors described a slowly adapting discharge, the endings of which had an arc of maximum sensitivity covering a few degrees of angular movement. They also stated, that there are endings in the medial collateral ligament and the patellar ligaments which could signal the tension of these structures.

In an important paper BOYD and ROBERTS (1953) reported their studies on the posterior nerve. They described both rapidly and slowly adapting sensory endings and analysed the slowly adapting ones. They showed them to be stretch receptors having a characteristic frequency for different positions of the joint, with "exaggerated" changes in frequency during movement. In 1954 ANDREW alone continued his studies on the medial ligament which he now showed to be equipped with Golgi endings giving a slowly adapting response.

BOYD (1953 b and 1954) correlated the physiological response with the histological structure of the endings in the posterior

part of the knee joint capsule. He states that the Ruffini endings give a slowly adapting response, the modified Vater-Pacini corpuscles a rapidly adapting response.

The authors mentioned above have so far only dealt with parts of the problem and they have worked on different nerves. Owing to this they have not been able to give a complete description of the behaviour of the sensory endings. It will be shown in this work that the sensory discharge in the medial and posterior nerves is fundamentally the same, and that the types of response are correlated with types of receptor with characteristic location —as shown in Chapter I—in the structures of the joint. The sensory endings have been found capable of measuring the position of the joint and also the speed and direction of a movement in the joint.

METHODS

Preparation: Successful recordings have been made in 98 cats 30 of which were used for experiments on the posterior nerve. Most of them were anaesthetized with nembutal 40 mg/kg body weight. Some were decerebrated under ether with the experiment delayed until 2 hours after the removal of the ether. No differences in regard to the sensory discharge from individual endings in the knee joint could be detected between the two types of preparation. In the decerebrate animal the muscle nerves, in the leg used, were cut to allow free movements of the joint. In some of the anaesthetized animals the muscle nerves were also cut.

Either the medial or posterior nerve to the knee joint was identified and dissected free. Its end was placed on a black perspex plate, on which further dissection with the aid of strong eyeglasses was carried out. The blood supply of the knee joint was kept intact as far as possible. If in an experiment with the medial nerve the genu suprema branch of the femoral artery was destroyed, the experiment was not continued on that knee.

The dissection having been completed in Ringer solution, the dissected nerves were immersed in paraffin pools, which were

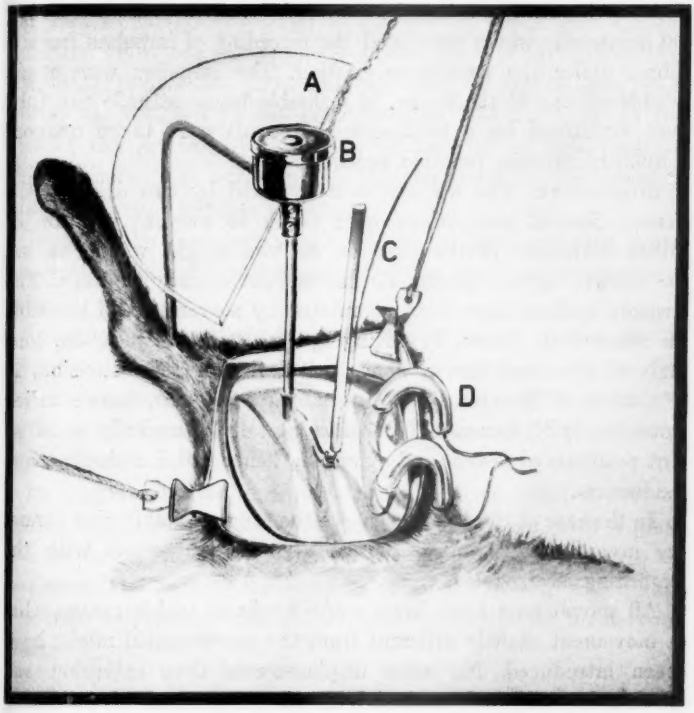

Fig. 12. Schematic drawing of the experimental arrangements for leading off action potentials in the medial nerve. (A, protractor for measuring degrees; B, potentiometer; C, recording electrode; D, heater coil.) A full description is given in the text.

made as deep as possible, sometimes by sewing a metal ring to the skinflaps and lifting them high. This arrangement allowed very large movements of the joint without uncovering the nerve.

The temperature of the paraffin was held at 37° C by a heater coil, glass-insulated (see Fig. 12) and fed by 24 volt D.C., the current being controlled by a variable resistor.

Recording device: Action potentials were led off with silver wire electrodes and fed to a push-pull amplifier through a cathode

follower input. The internal noise of the cathode follower reached 30 microvolts which prevented the recording of impulses from C fibres under the conditions existing. The impulses were made visible on one of the beams of a double beam cathode ray tube and monitored by a loudspeaker. Records were taken on continuously running bromide paper.

Stimulation: The leg was securely fixed by two drills in the femur. Special precautions were taken to prevent rotation or other deviations of the tibia by its own weight which, as will be shown, exerts specific effects on the sensory endings. The sensory endings have been stimulated by movements of the tibia in relation to femur: 1) Changing the angle between the long axis of tibia and femur, hence called flexion and extension. 2) Rotation of the tibia round its own long axis, hence called rotation. 3) Movements of the tibia laterally or medially at different positions of flexion and extension, hence called abduction and adduction.

In the case of the posterior nerve the range to full flexion cannot be investigated, because the tibia comes in contact with the recording electrode.

All movements have been made by hand which means, that a movement slightly different from the one intended might have been introduced. No other displacements than extension and flexion have been recorded. This simple method of producing movements was chosen because of the difficulty to design a machine that can produce large and constant movements of a limb. It was also soon found, that very little could be added to the results by studying constant speeds. To record small movements other than flexion and extension would be very difficult and has not been tried.

The movements were recorded by a linear potentiometer coupled over a battery. The axis of the potentiometer was fixed in a position which as near as possible concurred with the imaginary joint axis for flexion and extension through the condyles of the femur. The excursions of the tibia were transmitted to the potentiometer by a metal rod bent at right angles and fastened to the tibia (see Fig. 12). The differences in potential taken out from

the slide of the potentiometer as this moved were fed to a linear amplifier and made visible on the second beam of the oscilloscope. The deflection of the beam was calibrated in degrees read on a protractor fastened to the potentiometer (see Fig. 12). As the axis of the potentiometer cannot be fixed in an ideal position this introduces an error in the measurements of the absolute position of tibia relative to femur.

Because the movements were made by hand constant speed was never attainable and figures given for speed are approximate only.

In some of the experiments the effect of muscle tension on the receptors of the joint have been investigated by electrically stimulating nerves to muscles or by pulling on muscles which end in the joint capsule. In those cases both femur and tibia have been rigidly fixed.

In a great number of experiments where an isolated sensory ending was obtained the joint capsule was probed with a glass rod to determine the position of the ending and the type of response. The part of the capsule where the ending was found, was removed, stained with gold chloride and examined for nervous tissue.

RESULTS

The general discharge

Recording from the undissected medial nerve shows, that the greatest number of sensory endings are active when the knee is at maximal extension (Fig. 13 A). At maximal flexion a greater number of endings are active than in the mid-position between flexion and extension (Fig. 13 B), but they never reach the number at full extension. In the experiment where Fig. 13 was obtained, the muscles in the leg were denervated, and this reduces the number of endings firing in the mid-position.

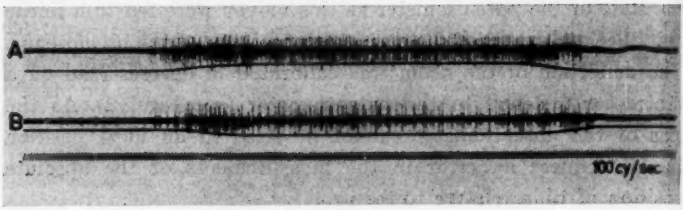

Fig. 13. Action potentials recorded in the medial nerve. A. The response to a movement of 20 degrees to full extension and back again (indicated by the signal line). B. The response to a movement of 20 degrees to full flexion and back again (indicated by the signal line). Time: 100 cy/sec.

In a few instances it has been possible to record separately from the upper and the lower branch of the medial nerve in the same animal. In both nerves sensory endings were firing in the extended as well as in the flexed position. These experiments have been too few for making any general statement, but sometimes it seemed that the lower branch was connected to more endings active at extension than was the upper one in which endings active at flexion were more numerous.

In the posterior nerve the discharge is increased at maximal extension. The position of maximal flexion cannot be investigated (see under Methods). Here also the resting discharge gets smaller in the mid-position if the leg is denervated, but never disappears altogether.

The discharge in the undissected nerves varied from animal to animal. Sometimes there were many endings connected to the nerves and sometimes few. This variation could of course also be due to fibres having been destroyed by the dissection or to unknown variations in the recording conditions, but it is most likely a reflection of the varying number of fibres in the articular nerves (see Chapter I).

When the tibia is rotated inwards or outwards, or ab- or adducted, in a position of extension or flexion, there are brought in additional sensory endings and the frequency of those already active is either increased or decreased. The latter is of course

more easily seen in a dissected nerve where there are only a few fibres responding.

Moving the tibia from the mid-position (undenervated muscles and some endings are responding) towards extension or in the medial nerve also towards flexion, more and more sense organs are brought into action.

The single unit discharge

By dissecting one of the nerves to the joint it has usually been possible to "isolate" the fibres of one or two active sensory endings (ADRIAN and ZOTTERMAN 1926; ZOTTERMAN 1936). As a rule this is easier to accomplish in the medial than in the posterior nerve because the whole range from flexion to extension can be investigated in the former. On the other hand the dissected posterior nerve may contain fibres connected to endings which are not active within the angle that can be investigated. This limitation of the investigation of the posterior nerve has been partly overcome by sewing a metal ring to the skin flaps and lifting them high, so that in one and the same preparation the angular range from 60 degrees of flexion to full extension could be examined without the posterior nerve becoming uncovered by paraffin.

Types of response. In both the posterior and the medial nerve two types of response have been found. 1) A slowly adapting response which can be activated by pressure on the joint capsule or ligaments or by movement within a certain angle of sensitive range from flexion to extension or by rotation in either direction. The critical angle is specific for each sensory ending. Furthermore within their range of critical angle the endings keep on signalling at a steady frequency for hours if after a period of adaptation from 0.5—1 min. they do not reach zero. The steady impulse frequency depends on the position within this angle. 2) A rapidly adapting response elicited only during a change in the tension of the joint capsule produced either by pressure or by movement. This response adapts to zero in less than one second.

The slowly adapting response

In Fig. 14 is shown a typical response from a slowly adapting receptor, in this case recorded in the medial nerve. Three spikes are discernible, one small from a slowly adapting sensory ending and two large spikes from rapidly adapting ones. We are here only concerned with the small spike. The particular sensory ending giving this action potential was active within an angle of 15 degrees, from 105 degrees to 90 degrees of extension. It could also be activated by inward rotation at full extension. In Fig. 14 the tibia was moved stepwise from 105 degrees to 90 degrees. In A the ending first was silent, then the tibia was moved 3 degrees to 102 degrees. A discharge was set up which early in B had adapted to a frequency lower than immediately after the movement in record A. Then the tibia was moved again, and the frequency went up during the movement and then adapted itself to the frequency at the beginning of the next record (C). This behaviour of the ending repeated itself in the following records up to F. The change of angle induced a higher frequency, which after the movement slowly diminished. In record F on the other hand the spike frequency at the completion of the movement went down instead of up. In G, it had set up a higher frequency than at the end of record F. Then a new movement in record G brought the tibia to an angle where the ending stopped discharging.

In Fig. 15 the movement was carried out in the opposite direction. Starting from 90 degrees of extension, where the sensory ending was silent, a movement of the tibia of 3 degrees to 93 degrees set up a discharge (A), which at the beginning of record B had adapted to a lower frequency. A new movement in B increased the frequency but at the beginning of record C it was higher still. During the movement in B one notices that the impulse frequency diminished. Then a new movement in C is seen to have slowed down the frequency, but at the beginning of record D it had again increased. A slowing down of the frequency during the movement and a following increase is seen to have

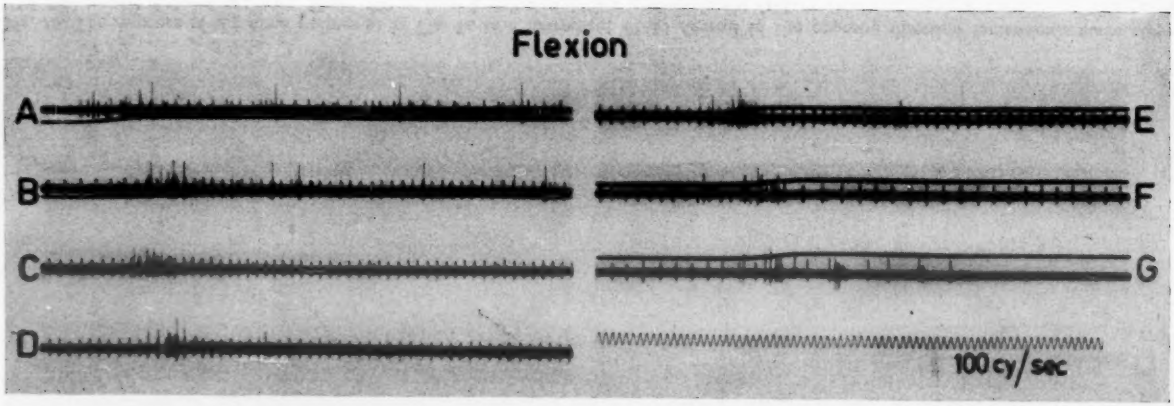

Fig. 14. One slowly adapting and 2 rapidly adapting endings recorded in the medial nerve on a movement of 15 degrees of flexion made stepwise (indicated by the signal line going upward). Time: 100 cy/sec. A full description is given in the text.

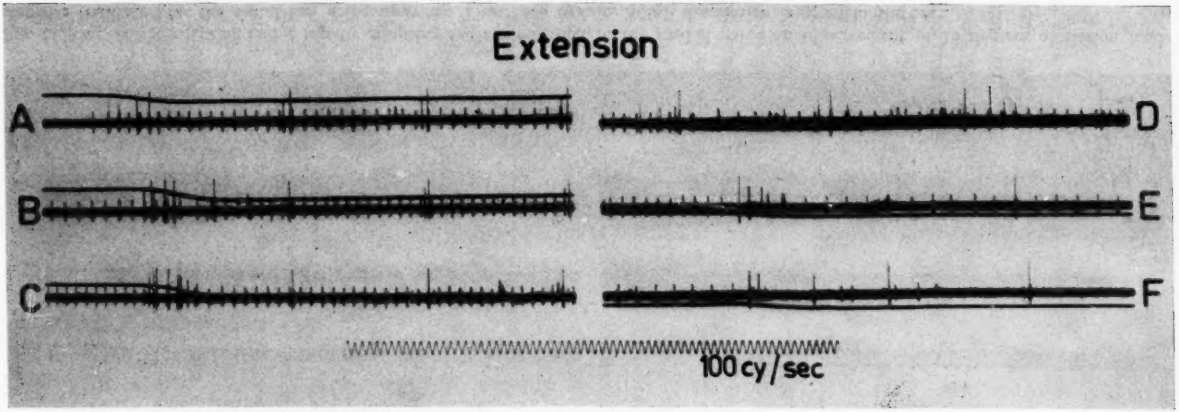

Fig. 15. The response of the same endings as in Fig. 14 to a movement of 15 degrees in the opposite direction (extension), made stepwise (indicated by the signal line). Time: 100 cy/sec. A full description is given in the text.

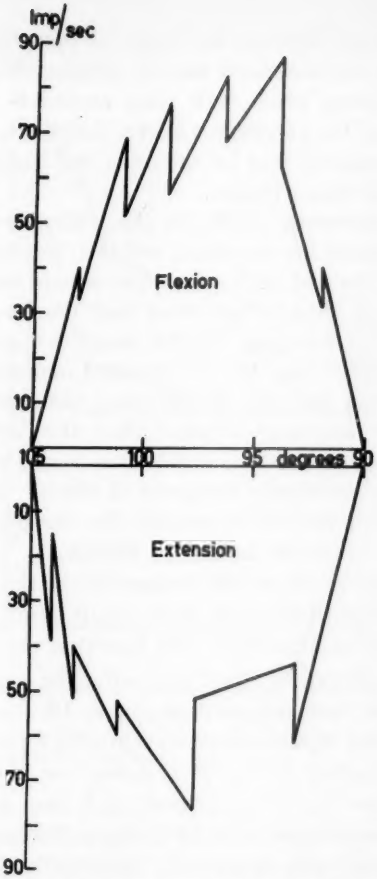

Fig. 16. Graphs of the response of the slowly adapting ending in Figs. 14 and 15. Impulse frequency is plotted against position in degrees. In the upper curve is shown the response to flexion and in the lower the response to extension. For description see text.

taken place in all the records from C to F, where the tibia has reached 105 degrees of extension and the discharge has stopped.

Plotting impulse frequency against position in degrees results in the curves shown in Fig. 16. The initial frequency is measured

from the intervals between the three to four first spikes immediately after the movement and the adapted frequency before the next movement which took place around 5—10 sec. later. A comparison of the two curves shows that the sensory endings behave in the opposite way for extension and flexion. The curves are approximate mirror images.

Thus in the movements of flexion the ending is seen to increase its frequency during the movement and then to adapt. The steady discharge also increases up to somewhere around 94 degrees where it becomes lower than before. After that the frequency rapidly falls to zero over 4 degrees. In this range the steady frequency is seen to be higher than the one obtained immediately after the movement. When the tibia is moved in the opposite direction (extension) the frequency obtained after the first 3 degrees of movement is higher than the steady frequency for that position, but after that the steady frequency is always higher than the one immediately after the movement. The turning point of these two curves is seen to lie around 94 degrees.

A comparison of the steady frequencies in the two curves at the same position shows them to be nearly identical. The differences are easily explained from the fact that the sensory ending has not been allowed to adapt fully after the movements which have not been made at constant speed. Of course the elastic forces in the joint capsule cannot be separated from the adaptation proper of the ending. In Fig. 17 is shown how impulse frequency depends on the rate of movement, and how adaptation time varies for different frequencies. In the figure the impulse frequency is plotted against time in seconds. The tibia is moved 5 degrees at 3 different speeds and the impulse frequency is determined immediately before and after the movement and then at the intervals shown in the figure. These curves clearly show, that the faster the movement, the higher the impulse frequency and the longer the adaptation time.

Fig. 18 shows the curves to movements at different speeds in the opposite direction. The opposite is happening to Fig. 17. The faster the movement, the lower the frequency immediately after

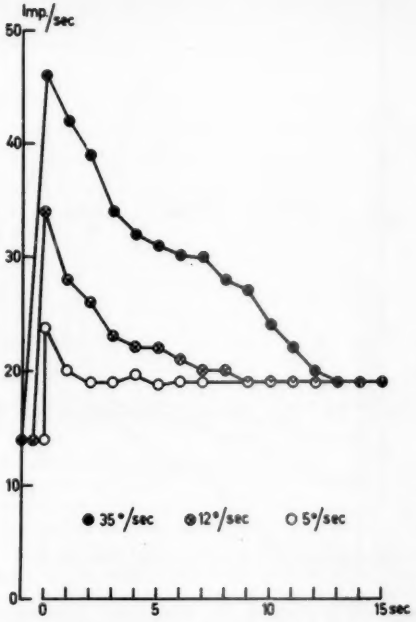

Fig. 17. Graph of the response of a slowly adapting sense organ to a movement of 5 degrees with different speeds. Impulse frequency is plotted against time in seconds. Each plot shows the decline in impulse frequency from the peak value attained at the completion of the movement.

the movement and at the fastest speed there is a silent period of 3 sec. For both these types of response, the increasing as well as the decreasing one, the change in frequency is greater the lower the initial frequency and in the case of a silent period this will be longer for movements of the same amplitude and speed. This behaviour reflects one of the fundamental properties of the slowly adapting sense organ, namely the differentiation by impulse frequency of different positions and the rather steep changes at both ends of the active range, as can be seen from the curves in Fig. 16. Figs. 17 and 18 show, that as soon as the ending is

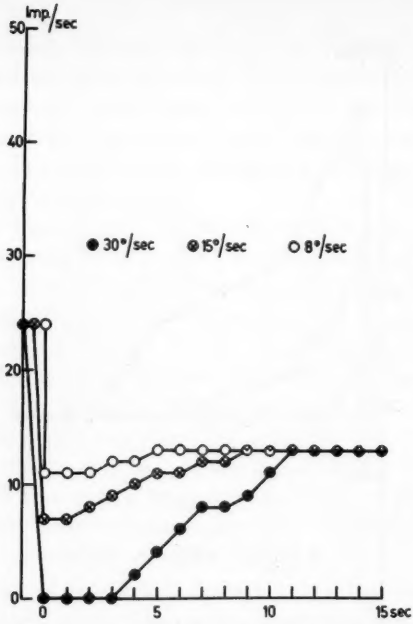

Fig. 18. Graph of the response of the same slowly adapting sense organ as in Fig. 17 to a movement of 5 degrees in the opposite direction with different speeds.

allowed full adaptation time its final frequency is the same independent of the speed at which the tibia reached the new position.

When moving the tibia through the critical angle for a particular sensory ending (its active range), it is found that the response always starts at a certain position which is independent of the speed at which the tibia traverses this angle, but the response in this position is not maintained, because of its low frequency. As a rule the response does not continue if the frequency is lower than 8—10 impulses per second. On the other hand, if the response is maintained over half a minute or so, it also goes on indefinitely with very small variations in frequency. Endings have been recorded firing at steady frequencies for 4—5 hours.

As can be seen in Fig. 19 there is considerable overlap in the critical angles of different sensory endings. The curves in Fig. 19

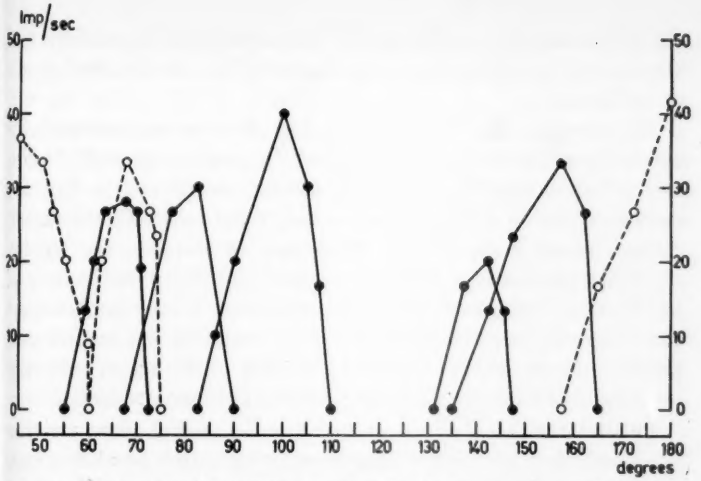

Fig. 19. Graphs of slowly adapting sensory endings in two experiments (full drawn lines from one experiment and dotted lines from another). The adapted impulse frequency is plotted against position in degrees for each sensory ending. The figure is not representative for the distribution of the endings in the range from flexion to extension. The endings which have their maximal adapted frequency immediately before or at full flexion or extension are more numerous than those lying in the range in between (compare Fig. 13). The sensitive ranges shown in the figure (15—30 degrees) are on the other hand representative of the behaviour of most endings.

are obtained from two experiments. The lines drawn in full are from an animal in which desheathing of the medial nerve had destroyed so many fibres that only five active endings were left. Two of them were active from 130—165 degrees of extension. When these two had been analysed the nerve was cut down further, and by luck the other three remained and were also easily recognizable by differences in size of their action potentials. The dotted curves are obtained from another experiment in which after dissecting the medial nerve three spikes remained. The points on the curves represent the steady frequencies at different positions for each ending. Fig. 19 shows that the critical angle varies between 15—30 degrees. The active range for a particular ending is practically never below 10 degrees. In this respect the curves are representative of most endings. On the other hand

the critical angle—as indicated by the findings in the undissected nerve—can be both widened and narrowed by rotation, abduction or adduction.

The curves in Fig. 19 also show that there are sensory endings which have their maximal adapted frequencies at full flexion and full extension. There are also (though not shown in Fig. 19) endings which have their highest steady frequency before maximal extension and flexion. These two types of response are by far the most numerous in both the medial and the posterior nerve, as indicated by observations on undissected nerves. Amongst these sensory endings, there are some, both in the medial and posterior nerve, which to judge by the size of the action potential are provided with large afferent fibres (ZOTTERMAN 1939).

Further analysis of the large spikes in the medial nerve arriving from endings with their maximum activity before or at maximal extension or flexion reveals features by which they differ from other slowly adapting sensory endings. Thus, if the medial collateral ligament is cut at its distal end, some of the sensory endings stop firing, but they can be brought into action again by fastening a thread to the ligament and loading it. In some instances it has been possible to isolate an ending associated with the medial collateral ligament, which was activated only at flexion or only at extension. On the other hand in those cases in which an ending was activated at both these positions it was never possible to determine with certainty if it was the same. The activity of these endings seems to be closely correlated with the tension of the medial ligament. Another property of these endings which supports this conclusion is that abduction of the tibia widens the angle within which such an ending responds. Adduction on the other hand reduces this angle. The response of some sensory endings giving large spikes activated by flexion can be altered by pressure on the patellar ligaments. Detaching the patellar ligaments and loading them has the same effect, but this procedure introduces too many errors as to which endings are activated, because the tension of the whole ventral part of the capsule is affected. Such effects are also sources of errors in experiments with the medial collateral ligament, but here they can be better controlled.

In the posterior nerve, as mentioned above, there are also large spikes from slowly adapting sensory endings responding at full extension, but there are also, contrary to those connected to the medial nerve, rather many that have their active range in the mid-position. Probing the joint capsule with a glass rod does not alter the response of some of these endings if the tibia is fixed. On the other hand they are extremely sensitive to rotation so that this movement one way can stop the discharge altogether, rotation the other way can increase it tremendously. In two experiments where pressure on the capsule did not produce any alterations in the frequency of this kind of large spike, it proved possible to cut loose the posterior part of the capsule without altering the response. This was tried with the medial side of the capsule in five other preparations in which the response likewise was unaltered by pressure on its posterior part and, again, the response remained unchanged. However, on continuing the dissection, the nerve was damaged. These experiments show that the action potentials did not arise in the posterior part of the capsule nor could they have emanated from the ventral side of the joint, which according to GARDNER (1944) should be innervated by the posterior nerve. In spite of the failure in some of the experiments to free the whole capsule while preserving the action potentials, these results suggest, that the endings responsible for this type of discharge are situated in the cruciate ligaments.

The slowly adapting responses arising from sensory endings in the ligaments have one feature in common. Contrary to the endings lying in the capsule itself their response to movement is sluggish and the difference between the adapted frequency and the one measured immediately after a movement is consequently small. The difference in frequency of response to different speeds of movement is also small. It also seems that their active ranges are larger than those of other slowly adapting endings.

The observation, made with undissected nerves, that cutting the muscle nerves diminished the number of sensory endings active can only mean that the muscles to some extent control

the tension of the joint capsule. In order further to elucidate this question the following experiments were made on the medial nerve. The femur was fixed in the usual way with two drills to the table. Through the tibia were inserted two other drills, one at its upper end and one at its lower. No movements of the tibia in relation to femur could therefore occur.

In four of the seven successful experiments performed in this way it was possible to isolate two spikes, one small and one large, from slowly adapting endings. The small spike showed alterations in frequency when either the quadriceps muscle or the adductor muscles were pulled upon or caused to contract by stimulating the femoral or the obturator nerve. The ending giving the large spike was not at all affected by this, but when the medial collateral ligament was cut, it stopped firing. In the other experiments of this type it was always possible to alter the response of some of the slowly adapting spikes, but those unaffected could not with certainty be shown to be associated with the medial ligament. Thus there are sensory endings which are influenced by the muscles which determine the tension of the joint capsule. On the other hand, at least some of the endings, associated with the medial and certainly those associated with the cruciate ligaments, remain uninfluenced by the tension of the joint capsule. No systematic investigation has been made as to which muscles are exerting influence on the tension of the joint capsule.

The maximal frequency of the slowly adapting sensory endings never exceeds 100 impulses per second after a movement, even when very high speeds are imposed. They are rather insensitive in their response to movements, but it has never been possible to measure an exact speed at which an increase of its rate of change does not increase the frequency. On the other hand, there is very little difference in spike frequency at different high speeds of movement. The large spikes associated with the ligaments seem, as mentioned earlier, to be the slowest in their response to movements.

No experiments have been made to find out the mechanical factors in the tissues underlying the response of the endings analysed here.

Fig. 20. The response of two rapidly adapting endings to a movement of 60 degrees made in steps of 20 degrees each. Time: 100 cy/sec.

Fig. 21. The response of the same endings as in Fig. 20 to a slow movement of 60 degrees. Time 100 cy/sec.

The rapidly adapting response

Both in the posterior and the medial nerve the slowly adapting response is accompanied by a rapidly adapting one. The spikes of the latter are usually larger than those from most slowly adapting endings (see Figs. 14 and 15). The rapidly adapting endings are activated by every type of movement of the tibia or even by a tap of the finger on the animal table. At certain positions of the joint one or two endings may be firing in synchrony with the pulse beat.

In comparison with the slowly adapting endings those giving rapidly adapting discharges are very few. In the experiments with cut muscle nerves, and the slowly adapting discharge in the mid-position between flexion and extension reduced to a minimum, it has sometimes been possible to isolate one or two spikes from rapidly adapting endings. Figs. 20 and 21 are from such an experiment in which after severance of the muscle nerves and dissection of the medial nerve only spikes from rapidly adapting endings were found in the angle from 100—160 degrees. On increasing the angle further a slowly adapting ending with its maximum activity at full extension started firing too (Fig. 22). In Figs. 20 and 21 are seen two spikes from rapidly adapting endings. The signal line indicates a movement from 160 degrees to 100 degrees, made in Fig. 20 in three steps of around 20 degrees each. It is seen that the response stops immediately after the movement. In Fig. 21 the joint is moved slowly and continuously through the same 60 degrees as in Fig. 20 and the large spike is seen to fire eight times, the small only once. A glance at the two figures shows that the frequency depends on the rate of the movement. In this case the movements were made in the same direction but the general relation of frequency to speed of movement is more or less independent of the direction of the movement.

Fig. 22 shows the slowly adapting discharge that started firing at 160 degrees. In A the tibia is moved slowly from 165 degrees to 160 degrees and the slowly adapting ending stops firing. An additional rapid movement is seen to activate spikes from the

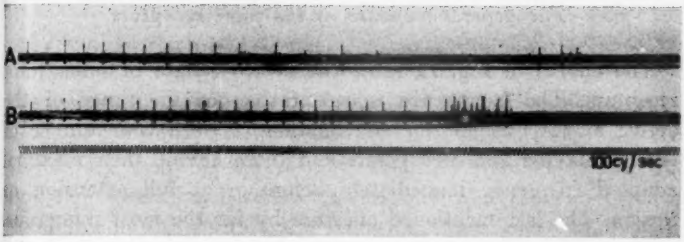

Fig. 22. The response of one slowly adapting sensory ending and two rapidly adapting ones from Fig. 20 and 21. A. Slow movement from 165 to 160 degrees. The slowly adapting ending is seen to stop firing. An additional small but quick movement activates the rapidly adapting endings. B. Movement through same angles as in A, but faster, is seen to activate the two rapidly adapting endings. Time: 100 cy/sec.

rapidly adapted endings analysed in Figs. 20 and 21. In B the same movement is produced again, but faster, and the rapidly adapting organs are now activated in a movement from 165 to 160 degrees owing to the greater speed of the movement. The size of the action potentials in the two types of response are of the same order. The slowly adapting ending was found to be associated with the medial collateral ligament.

The relation of the slowly to the rapidly adapting endings seems to be of some interest, so that whenever it has been possible to isolate one of each of these two types of discharge, they have been compared. As a rule it can be said that the rapidly adapting endings are only activated, when the stimulating movement has reached a speed which is able to produce a marked decrease of discharge rate or a silent period in the response of a slowly adapting ending. In the opposite direction of movement the rapidly adapting ending is maximally activated, when the speed of the movement has risen to a degree at which there is only a small difference in the frequency of the slowly adapting spike to an even faster movement. The activation of the rapidly adapting endings in relation to the slowly adapting ones is, however, more easily observed in the case where the movement produces a decrease of the latter.

The curves in Fig. 19 show the active ranges of some joint receptors. The curves are representative for the range of the active angles but not for the relation between the number of endings having two zero points and those having their maximal adapted frequency immediately before or at full extension or flexion. The last mentioned ones are by far the most numerous.

The endings having their maximal frequency at full flexion or full extension will always respond with an increase to a movement in one direction and with a decrease to a movement in the opposite direction.

The rapidly adapting responses also give an easily interpretable pattern. As a rule these endings can be activated by a fast movement at any position of the joint and give rise to a discharge that is more or less equal to movements in both directions.

On the other hand the endings which have two zero points will respond in succession with an increase and a decrease in its frequency to a movement in one direction. This will also be the case with those endings (not shown in the curves of Fig. 19) which reach their maximal frequency before full flexion and full extension. So far the endings have been analysed individually. On account of the variation in the nerve supply to the knee joint (Chapter I) and the technique used to study the endings it has not been possible to obtain a picture of the whole afferent inflow from the joint.

It has only been possible to study either the medial or the posterior nerve at the same time, and in each nerve only one or a few endings can be analysed in detail. However, it can be stated that over the whole range from flexion to extension the active ranges for different endings are overlapping, and this stands for both types of slowly adapting endings as far as it has been possible to investigate the posterior nerve. The endings associated with the ligaments seem to be arranged principally so, that those in the medial nerve cover the ranges at flexion and extension and those in the posterior nerve the range in between.

The correlation between physiological response and anatomical type of sensory ending

From the results given in Chapter I, namely that only Golgi endings are found in the ligaments, it is obvious that some of the slowly adapting spikes must originate from those. To find out the correlation between the response and the two types of receptors in the capsule the following experiments were made. When a single spike preparation had been obtained the joint capsule was probed with a glass rod to locate the ending responsible for the discharge and to classify the type of the response. This part of the capsule was then removed and stained with the gold method used in Chapter I. A great number of such experiments have been made. It was soon found that it was difficult to locate

Table IV

	Posterior part of the capsule	Anterior part of the capsule
1. Slowly adapting response . .		Ruffini
2. „ „ „ . .		Ruffini
3. „ „ „ . .		Ruffini
4. „ „ „ . .		Ruffini
5. „ „ „ . .		no nervous tissue
6. „ „ „ . .		no nervous tissue
7. „ „ „ . .		unidentified
8. „ „ „ . .	Ruffini	
9. „ „ „ . .	Ruffini	
10. „ „ „ . .	Ruffini	
11. „ „ „ . .	Ruffini	
12. „ „ „ . .	unidentified	
13. „ „ „ . .	Ruffini	
14. „ „ „ . .	Ruffini	
15. Rapidly adapting response .		Vater–Pacini
16. „ „ „ . .		no nervous tissue
17. „ „ „ . .	Vater–Pacini	
18. „ „ „ . .	Vater–Pacini	
19. „ „ „ . .	unidentified	
20. „ „ „ . .	no nervous tissue	

one single ending other than in the outer zone of the areas outlined in Figs. 5 and 7 (Chapter I) where the endings are more sparse. In these regions the piece of capsule taken out has sometimes been sufficiently small to contain only one single ending, although there have often been other nerve fibres passing by. The table presented above from 20 animals is representative for the findings in the experiments of this type after the method had been worked out sufficiently.

From the table it emerges that the slowly adapting discharge is associated with the Ruffini ending and the rapidly adapting one with the modified Vater-Pacini corpuscle. Both these types of ending were found in the areas of the capsule determined in Chapter I (Figs. 5 and 7). It is worth noticing that in these experiments the capsular endings were extremely sensitive to very light pressure with a glass rod. This again points to the possibility of a strong effect from the muscles on the response of endings sensitive to small variations in the tension of the capsule.

DISCUSSION

The undissected medial nerve shows a maximum of impulse activity as the tibia reaches full extension or full flexion, as also observed by ANDREW and DODT (1953). In the posterior nerve the maximum of discharge also occurs at full extension. This brings up the question of whether the sensory endings firing at extension are the same as those firing at flexion. ANDREW (1954) described a receptor connected with the medial nerve which was firing at a load of 5 grams on the medial ligament in situ. Within a range of tension from 5 to 90 grams the ending was silent. Beyond 90 grams' tension it again started firing. ANDREW thought that this would account for the discharge of nerve impulses in a fibre, when the joint is moved away from the mid-position either towards flexion or extension. Yet ANDREW only saw the type of receptor described above with ligaments in situ, and thus could not exclude having stimulated endings outside it. To judge by the curves of Fig. 19 the general organisation of the sensory

responses is different. Furthermore, the observation that the frequency of some of the endings firing at flexion can be altered by pressure on the patellar ligaments, whilst the discharge of some of those responding to extension is altered by pressure on the medial ligaments, is also in favour of the concept that there are different endings signalling different positions.

The relation between physiological response and anatomical type of sensory endings

The results presented in this work and in that of BOYD (1954) make it certain that the slowly adapting responses arising in the joint capsule come from the Ruffini endings and the rapidly adapting responses from the modified Vater-Pacini corpuscles. From the work of ANDREW (1954) on the medial ligament and the results presented here it can also be concluded that some of the slowly adapting responses, which differ from the others by being slower in recording movements, arise in the Golgi organs of the ligaments.

The slowly adapting discharge

By far the most numerous of the sensory endings have their maximal adapted frequency at a position immediately before or at full extension, in the medial nerve also before or at full flexion. The analysis of all the slowly adapting sensory endings shows them to behave as stretch receptors and they have characteristic features in common with other stretch receptors, for instance those in muscle (MATTHEWS 1933). They deliver a sustained discharge to continuous stimulation, and a change in stimulation produces either an increase or a decrease in frequency depending upon the direction of the movement. The changes of frequency are related to the rate of change of the movement. The frequency during a change differs from the frequency set up by constant stimulation at the new position reached. No attempts have been made either to distinguish mechanical factors of adaptation of the tissue from

physiological ones arising in the design of the receptive structure or to find out the general relation between the behaviour of the endings in terms of mechanical forces in the tissue. In view of the orientation within the capsule of such complicated sensory units as for instance the one shown in Fig. 9, Chapter I, evaluation of the mechanical factors encounters formidable obstacles.

One of the fundamental features of these sensory endings seems to be that they are active only within certain critical angles for which they have an adapted impulse frequency, different for different positions within it. ANDREW and DODT (1953) in studying the endings connected with the medial nerve published curves showing the impulse frequency of different endings at different positions of the tibia. From their results it is, however, impossible to form a clear concept of the behaviour of these endings. Their curves point to critical ranges of two to three degrees, but they do not show if the endings, after having reached their maximal discharge, continue firing at the same frequency, and how far they are from their zero point. In one of the curves, however, the ending is seen to fire with the same impulse frequency over nearly four degrees. Neither do they describe the decrease of frequency (or silent period) that should appear in investigating the whole critical range with movements of opposite direction. The inconsistencies and deficiencies of their findings might be explained by their having rotated the tibia, which sometimes decreases the active range, or adducting the tibia which alters the behaviour of the endings connected with the medial ligament.

The results of BOYD and ROBERTS (1953) concerning the endings connected with the posterior nerve and lying in the capsule are confirmed in this work. Only a few points will be discussed in this connection. These authors never studied an ending over its whole active range. The reason for this is firstly, that they did not study large angles of movement, secondly that they were working only on decerebrate cats and were always forced to denervate the muscles to allow free movements of the leg. Thus in their experiments the tension of the joint capsule could have been altered so that the sensory endings got a wider range of activity than normal.

Another point that deserves discussion is that BOYD and ROBERTS never attempted to investigate if impulses arise outside the joint capsule, that is to say from the cruciate ligaments. It might be of interest to notice that one third of their endings were activated only by rotation. This could be explained by their leading off from fibres of the Golgi endings of the cruciate ligaments, which give the largest action potentials. Since the whole range of movement in the joint was not tested, these endings might have had their critical angle outside the range studied and may therefore have been activated only by rotation, which alters the tension of the cruciate ligaments. BOYD and ROBERTS state that all the endings they were studying were situated in the capsule, but they do not say if they fixed the tibia when exerting pressure on the capsule.

The existence of two types of slowly adapting response in the joint has been emphasized by ANDREW (1954). He found that the ligament endings were not as sensitive to movements as the capsular units. This observation is confirmed in the present work. BOYD (1954) pointed out that the tendon organs in muscles were slower in their response than the capsular endings.

The influence of the muscles on the discharge observed in the undissected nerve was found, in the dissected nerve, to be principally restricted to the endings lying in the joint capsule but those in the patellar ligaments will very likely be influenced too. Some at least of the endings associated with the medial collateral ligament and certainly those associated with the cruciate ligaments are uninfluenced by the muscles. This has also been pointed out by ANDREW (1954) with regard to the medial ligament.

The rapidly adapting response

The rapidly adapting response emanating from the modified Vater-Pacini corpuscles of the joint discharge in a way familiar from other Vater-Pacini corpuscles (GRAY and MATTHEWS 1951 a; GAMMON and BRONK 1935; GERNANDT and ZOTTERMAN 1946). It is of some interest in this connection that the joint corpuscles can be activated by every type of rapid movement whatever the

position of the joint at the start. For this reason these endings may be of great importance though by no means numerous. Another significant feature is that the movement which activates them must have reached a certain minimal speed, and that movements of such rates also produce great variations in the response of the slowly adapting endings. Thus the rapidly adapting sensory endings will fill in the first part of the silent period seen in a decrease of the slowly adapting response or add to the slow increase by which the latter responds to a fast movement in the opposite direction. The well-known dependence of the response from pacinian corpuscles to rates of change of the stimulus has been analysed by GRAY and MALCOLM (1950) and GRAY and MATTHEWS (1951 b).

The physiological role of the joint receptors

As pointed out both by ANDREW and DODT (1953) and BOYD and ROBERTS (1953), the joint receptors inform the central nervous system about the relative position of the bones of the joint and the speed of movement in this same joint. To this should now be added, as shown above, that these receptors also can signal the direction of a movement, appearing as an increase of frequency in one direction and a decrease in the opposite direction. This new attribute of the joint receptors may well be of considerable importance (see General Discussion). Emphasis should also be laid on the muscular control of the joint receptors. In conjunction with earlier findings the results gathered in this work make it possible to discuss in detail the measuring functions of the joint receptors as revealed in the periphery by spike recording.

It is convenient from the point of view of function to divide the responses into three types: 1. The slowly adapting discharge arising in the ligaments; 2. the slowly adapting discharge arising in the capsule; 3. the rapidly adapting response. This functional subdivision corresponds directly with the different histological structures of the joint endings.

The type 1, the Golgi ending, signals direction of movement but, being uninfluenced by the muscles, its main function will be

to reveal position. The slow behaviour of the type 1 receptor in response to movement will make it less qualified to signal speed. The type 2, the Ruffini ending, like type 1, signals direction of movement but its main function, owing to its greater sensitivity to movement, will be to record the speed of the movement. Being influenced by the muscles it is less suitable for measuring absolute position, but does well with changes of position. Type 3, the modified Vater-Pacini corpuscle, is activated by quick movement independent of its direction and contributes to the discharge signalling speed of movement. It thus serves as a kind of acceleration receptor.

It is interesting to note the narrow ranges within which many joint receptors are active and the large number of such specific ranges (Fig. 19). As pointed out by GRANIT (1955) this is a characteristic solution of the problem of specificity whenever it is required to carry out important tasks of discrimination in a sense organ. Such narrow sensitivity bands occur in the eye, the ear and in the temperature sense, as recently shown by ZOTTERMAN and coworkers (1953).

The organisation and properties of the joint receptors for measuring position, direction of movement and its velocity recur in other sensory systems concerned with analogous problems. COHEN (1955) investigated the statocyst organ of the lobster Homarus americanus and found four types of receptors of which the first two behave like the Golgi and the Ruffini endings. COHEN's type 3 and 4 are termed acceleration and vibration receptors respectively. These functions are in the joint receptors both fulfilled by the rapidly adapting modified Vater-Pacini corpuscles.

As pointed out by ANDREW and DODT (1953) and ANDREW (1954) the receptors in the ligaments should be the true position receptors. Since these are uninfluenced by the muscle tone it seems likely that they signal the absolute position. The concept of BOYD and ROBERTS (1953), who studied only capsular endings to which they attributed the property of recording position, seems less attractive, knowing as we do now that the joint capsule is sensitive to muscle tension. The experiments already described

(and continued in Chapter IV) show that an increase or a decrease of the tension in the joint capsule shifts the critical angle of its sensory endings. These endings may of course also be able to control the muscular tone.

This concept of the joint receptors as recorders of joint position, speed of movement and direction of movement can thus be attained from the study of single receptors. How these functions are integrated in the periphery by all the sensory endings working together is another matter. The spatial relationship of the joint receptors as well as the ability of some endings to give opposite responses to a movement in one direction must, however, produce a rather complicated sum total.

SUMMARY

1. The properties of receptors of the knee joint of the cat were analysed by recording action potentials in the medial and posterior nerves, and the physiological responses were related to the sensory endings present in the joint.

2. There is a maximum of impulses from the medial nerve when the tibia is at full flexion or full extension and in the posterior nerve as the tibia reaches full extension. In the posterior nerve the situation at full flexion cannot be investigated with the recording technique used.

3. Both in the medial and the posterior nerve one can record responses from slowly and rapidly adapting receptors.

4. The responses are divided into three categories, which can be related to the different types of sensory endings, present in the joint. The histological investigation in Chapter I has shown that the ligaments are equipped only with the so-called Golgi tendon organs. These endings are responsible for one type of slowly adapting response. The other slowly adapting response arises from the Ruffini endings in the joint capsule. The rapidly adapting response emanates from the modified Vater-Pacini corpuscles.

5. The type 1 receptor is the slowly adapting Golgi ending which, associated with the ligaments, works uninfluenced by muscles and thus records the exact position of the joint. It also records the direction of movement, but its low sensitivity to movement as such makes it less adequate to signal the speed of movement.

6. The type 2 receptor is the slowly adapting Ruffini ending which lies in the capsule. It signals the direction of movement and, owing to its considerable sensitivity to movement, it can also signal speed of movement. The type 2 receptor works under the influence of those muscles which alter the tension of the joint capsule. As long as it is unknown what influence these receptors exert upon the muscular tone, they cannot be regarded as true position receptors. Yet they will signal minor variations of position as movement.

7. The type 3 receptor is the Vater-Pacini corpuscle giving rise to the rapidly adapting response. This receptor is very sensitive to quick movements independent of their direction, and its discharge adds to the one set up by fast movement. It will thus serve as an acceleration receptor. It is also sensitive to vibration.

CHAPTER III

Pathways for afferent fibres from knee joint to spinal cord

For the study of reflex effects of the nerves of the knee joint on its extensors and flexors, it is of interest to know by which dorsal roots the fibres of the medial and posterior nerves enter the spinal cord. Stimulating the ventral roots will also clearly show, if in the direct articular nerves there are any efferent fibres distributed to muscles around the joint.

GARDNER (1948) studied the conduction rates and dorsal root inflow of articular nerves from the knee joint in the cat. He reported, that impulses from the posterior nerve enter the spinal cord over the 6th and 7th lumbar and sometimes the 1st sacral dorsal roots, and impulses from the medial nerve over the 5th and 6th lumbar dorsal roots. He did not stimulate the ventral roots. His statement that the largest fibres do not have the lowest threshold is contrary to common experience of electrical stimulation of nerves and raises the question whether spread of current, and thus inadequate stimulation might have occurred in his experiments. This makes his findings on the root distribution of the nerves doubtful.

METHODS

Experiments were performed on 35 cats anaesthetized with nembutal 40 mg/kg body weight. The spinal cord was exposed by a large laminectomy in the lumbar region, and the dorsal and

ventral roots L 4, L 5, L 6, L 7 and S 1 were identified and cut free from the spinal cord. Either the medial or posterior nerve was dissected free and cut peripherally. All exposed nerves were kept warm with paraffin oil at 37° C. Either the dorsal or the ventral roots were stimulated with square waves of less than 0.5 milliseconds' duration, and action potentials were led off from the articular nerves in the manner described in Chapter II. After the experiment the nerves were dissected free, and the conduction distances measured.

RESULTS

Stimulation of ventral roots

On stimulation of the ventral roots L 4, L 5, L 6, L 7 and S 1 no action potentials were obtained either in the posterior or the medial nerve.

Stimulation of dorsal roots

On stimulation of the dorsal roots L 5, L 6, L 7 and S 1 action potentials were recorded in the articular nerves.

The posterior nerve. Action potentials were always recorded in the posterior nerve following stimulation of the L 7 and sometimes the S 1 dorsal root. Stimulation of the roots L 6 or L 5 never gave any action potentials in the posterior nerve. As a rule the conduction distances were long enough to separate four groups of different conduction rate in the compound potential. The distances ranged from 14.5—17.5 cm. There is first a component conducting at 80—100 m/sec., then a second one conducting at 40—80 m/sec., and a third conducting at between 20—40 m/sec.; then minor deflections follow which are very variable and represent rates of conduction from a few to 20 m/sec.

The medial nerve. In the medial nerve, owing to longer conduction distances, it was often very much easier to separate the different groups in the compound potential. These ranged from

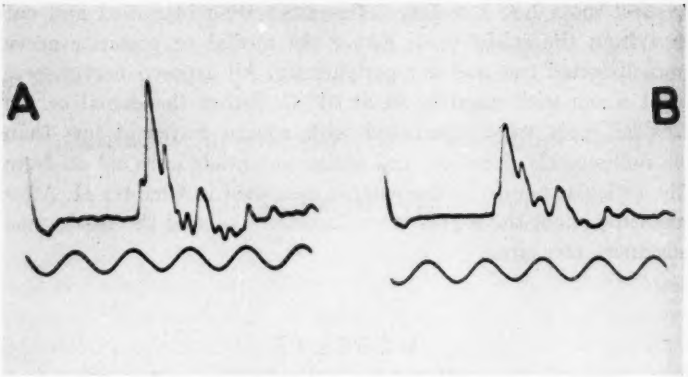

Fig. 23. Recording from the posterior nerve on stimulation of (A) L7 dorsal root, (B) S1 dorsal root showing the main deflections. Time: 1 000 cy/sec.

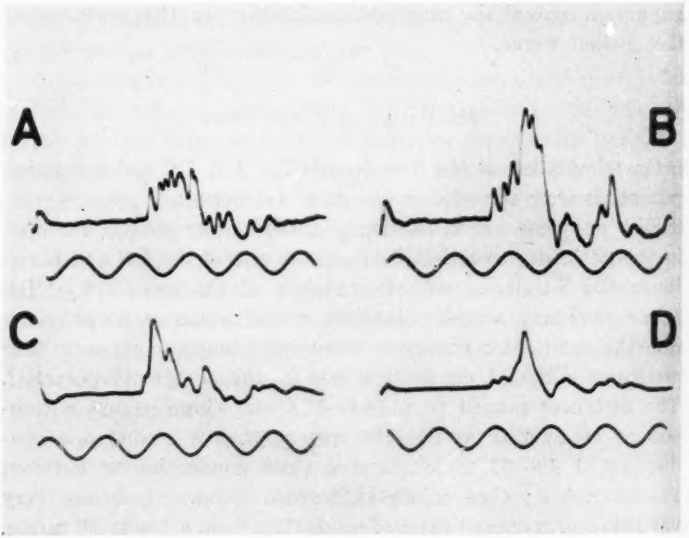

Fig. 24. Recording from the medial nerve on stimulation of (A) L5 dorsal root, (B) L6 dorsal root. In C and D the same stimulation and recording as in A and B after cutting the obturator nerve. Time: 1 000 cy/sec.

17—21 cm. Action potentials were always recorded on stimulation of the L 5 and sometimes of the L 6 dorsal root. The recorded action potential was sometimes very complex and in those cases the medial nerve derived from both the saphenous and the obturator nerve (Fig. 24). In two cases the whole medial nerve derived from L 5 only and in two other cases the whole nerve derived from the obturator nerve. The major elevations, when the medial nerve derived entirely from the saphenous or obturator nerve, were four. A first small initial component had a conduction rate of 80—100 m/sec., a second 40—80 m/sec. and a third 20—40 m/sec. At last followed variable waves conducted at rates from a few to 20 m/sec.

DISCUSSION

It is evident from the experiments with stimulation of ventral roots that the joint nerves do not contain any somatic efferent fibres.

In this investigation no action potentials were obtained in the posterior nerve on stimulation of the 6th lumbar dorsal root. GARDNER (1948) stated that he consistently recorded action potentials in the posterior nerve on stimulation of dorsal root L 6. The wide variation of the joint innervation seen in the periphery may, of course, have its counterpart in the dorsal root distribution, but it is nevertheless remarkable that of 20 cats used for experiments on the posterior nerve, none was seen to have any fibres of this nerve in the 6th lumbar dorsal root. As noted above, GARDNER's statement that the fastest fibres do not have the lowest threshold suggests that spread of current might be the explanation of his results.

The conduction rates of the afferent joint fibres are in good agreement with the calibre spectra of the joint nerves. If the relation between fibre diameter and conduction rate is assumed to be linear (GASSER and GRUNDFEST 1939) and the HURSH constant of 6 (HURSH 1939) is used the first elevation in the

potential is from fibres between 13—18 microns, the second is derived from fibres between 7—13, and the third from fibres between 3—7 microns. The fourth elevation should then be derived mainly from the unmyelinated fibres.

SUMMARY

1. Action potentials have been recorded in the medial and the posterior nerves on stimulation of various spinal nerve roots.

2. Stimulation of the ventral roots L 4, L 5, L 6, L 7 and S 1 give no action potentials in either the medial or the posterior nerve. The articular nerves thus contain no somatic efferent fibres.

3. Action potentials were always recorded in the medial nerve on stimulation of the 5th lumbar dorsal root and sometimes the 6th. The posterior nerve was always represented in the 7th lumbar dorsal root and sometimes in the 1st sacral.

4. The conduction rates are in good agreement with the calibre spectra of the articular nerves presented in Chapter I.

CHAPTER IV

The relation of joint receptors to muscles

GARDNER (1950) studied the reflex effects on stimulation of knee joint nerves in the cat. He stimulated the posterior and the medial nerve in decerebrate and decapitate animals and observed the responses of various muscles. In the decerebrate preparations he found very variable effects on stimulation of the large articular fibres. In the decapitate animals stimulation of the large fibres consistently gave a flexor reflex.

Because GARDNER only noted the visible contractions of the muscles, his results are difficult to evaluate. The reflex effects, of the large articular fibres on the flexors and extensors of the knee joint must be studied with a more sensitive method. The size of the monosynaptic potential (ECCLES and PRITCHARD 1937), elicited from a muscle nerve and recorded from a ventral root, can be used as a test of the effects of different afferent fibre systems on motoneurone excitability (RENSHAW 1940; LLOYD 1943 a, b and c; HAGBARTH 1952).

The aim of the experiments to be presented has not been to uncover the effects of joint receptors on all phases of muscle action in locomotion. However, experiments reported in Chapter II have shown that joint receptors signal position and movement of the joint. The study of the reflex effects elicitable from joint nerves will, besides supporting the results in Chapter II, show that the receptors in the joint already at the spinal level are involved in controlling position and movement. It will also be possible to attribute to some of the receptors in the knee joint the ability of signalling resistance to movement.

METHODS

The animals used in these experiments were all decerebrated under ether after ligation of the carotid arteries. Two hours were allowed for the ether to be removed before the experiment started.

In one series of experiments most of the animals were made spinal by a section at Th. 10. The spinal cord was exposed in the lumbar region, and the ventral roots L 5—S 1 on one side were cut and dissected free for recording of the monosynaptic potential on their central stump.

During the experiments the animals were placed on a heated table and the exposed tissue kept warm with paraffin at 37° C. The rectal temperature was always controlled and sometimes the blood pressure.

Monosynaptic potentials were elicited by electrical stimulation from the quadriceps, gastrocnemius and the biceps-semitendinosus muscles. The two latter represent flexors of the knee joint, and the former an extensor. The rectus femoris is also a flexor at the hip joint and was usually excluded. The gastrocnemius is also an extensor of the ankle joint.

The animals were prepared differently depending on whether the conditioning stimulus of the articular fibres was elicited by electrical stimulation or by natural stimulation of the joint receptors.

Electrical stimulation. All the nerves in the limb used were cut. The appropriate muscle nerves and the medial or the posterior joint nerve were dissected out. The conditioning stimulus on the joint nerve was a square wave of 0.5 milliseconds' duration which could be delivered either as a single shock or a tetanus. The test shock on the muscle nerve was delivered by a thyratron stimulator. The shocks were triggered by a delay circuit and the sweep started simultaneously with the conditioning stimulus. The stimulating electrodes were small silver silver-chloride hooks with an interpolar distance of 2—3 mm for the joint nerve and of about 5 mm for the muscle nerve.

The threshold stimulus for the joint nerve was determined by

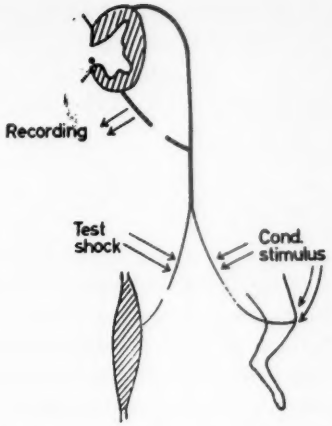

Fig. 25. Diagram illustrating the experimental arrangement when the monosynaptic method is used.

leading off directly from this nerve which was dissected free over as long a distance as possible. Spread of current was controlled by recording from bigger nerve branches and the conditioning stimulus was set to slightly above threshold.

Adequate stimulation. In these experiments the knee joint was placed at different positions to set up conditioning impulses in the articular nerve fibres, taking the mid-position where few endings are active as the reference position. Extensive denervations were carried out in the limb used. All nerves except the medial joint nerve were cut and the appropriate muscle nerves dissected free. All dorsal roots in the lumbar region except L 5—S 1 on the experimental side were severed. The limb was securely fixed by a drill through the hip joint and one through the lower part of the femur. Test shocks were delivered to the muscle nerves each second, and monosynaptic potentials were recorded from the ventral roots while the tibia was moved and set at different positions. Movements of the tibia were made by hand and recorded in the way described in Chapter II. (Fig. 25 illustrates the arrangement when the monosynaptic method is used.)

In one series of experiments only decerebrate cats were used and all nerves kept intact except the medial one which was dissected free and cut. Action potentials were recorded from the peripheral stump of this nerve in the way described in Chapter II.

RESULTS

Electrical stimulation of the joint nerves. In these experiments a single shock or a tetanus was applied to a joint nerve and the ensuing excitability changes of the motoneurones of the muscles were tested by the size of their monosynaptic potentials 4—80 milliseconds after the conditioning stimulus. A complicating factor in these experiments is the wide variation of the pathways to the spinal cord for the fibres from the medial nerve. Sometimes the whole medial nerve or a portion of it reaches the spinal cord via the obturator nerve which, however, always has to be cut.

Single shocks or a tetanus applied to the joint nerve gave very small and variable effects, both in the decerebrate and the spinal preparation. Very often no effects were obtained although stimulation of different skin nerves definitely influenced the size of the monosynaptic potential (HAGBARTH 1952). The effects elicitable from a joint nerve were, when present, usually small and consisted of either excitation or inhibition of extensors and flexors, always in a reciprocal fashion. If, for instance, the effect on the quadriceps was facilitation, the effect on the biceps-semitendinosus was always inhibition. Consistent effects on flexors and extensors to stimulation of either the medial or the posterior nerve were not seen from animal to animal. When effects were present they were, however, always reciprocal and decreased with time after the conditioning stimulus, disappearing after 40—50 milliseconds, when they fell to the control level of the monosynaptic potential.

With the conditioning stimulus used in these experiments the effects were either facilitation or inhibition. Inhibition followed by facilitation or vice versa was not seen, but sometimes the effect did not turn up clearly until after 10—15 milliseconds

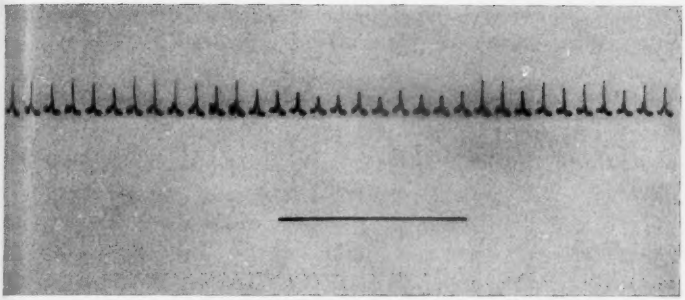

Fig. 26. Spinal cat. Monosynaptic test reflex elicited from the quadriceps nerve once per second and recorded from the ventral root L6. The monosynaptic potential is inhibited by pressure on the joint capsule indicated by the signal line.

after the conditioning stimulus, but in the meantime the monosynaptic potential was of the control size.

Adequate stimulation. In these experiments a test shock was delivered to a muscle nerve each second, and the ensuing monosynaptic potential recorded from the ventral root while the tibia was set at different positions. Only the medial nerve was studied in this way, because it is very much easier to denervate the limb totally and leave only this nerve than to retain the posterior nerve alone.

Using adequate stimulation of the joint receptors has of course the drawback, that the denervation of other structures than the one investigated can never be done carefully enough. The fixation of the animal has to be very firm. To make certain that the effects studied are set up by the joint endings, they must disappear after cutting the joint nerve.

To decide if at least some of the effect emanated from the joint, before this could be controlled by section of the joint nerve after the experiment, the following procedure was adopted. At the beginning of each experiment light pressure was exerted on the joint capsule to see if any changes of the monosynaptic potential, elicited from one of the muscle nerves, could be set up by this kind of stimulation which could not activate endings outside the joint. Fig. 26 shows an effect on the monosynaptic

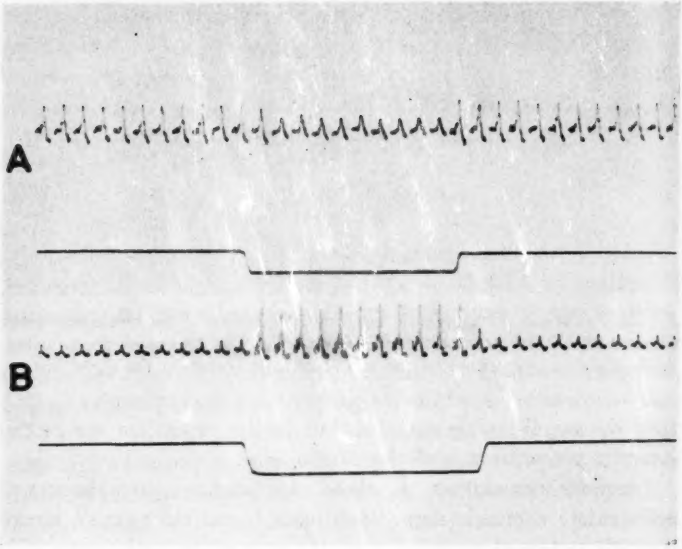

Fig. 27. Spinal cat. Monosynaptic potential elicited once per second, A, from the quadriceps muscle, and recorded from L6 ventral root, B, from the gastrocnemius muscle, and recorded from L7 ventral root. The quadriceps reflex is inhibited and the gastrocnemius reflex facilitated by altering the position of the tibia from 165 degrees to full extension as indicated by the signal line.

potential elicited from the quadriceps nerve and recorded in the ventral root L 6. This was produced by pressure on the joint capsule in the region of the medial collateral ligament.

Fig. 27 shows the monosynaptic potential of the quadriceps (A) and gastrocnemius (B), first when the tibia is at a position of 165 degrees relative to the femur. Then the position is changed to 180 degrees (full extension) and then back again to 165 degrees, as indicated by the signal line. There is an inhibition of the quadriceps and a facilitation of the gastrocnemius at the position of 180 degrees compared to the position of 165 degrees. In this same experiment the position of full flexion gave a small facilitation of the quadriceps and a likewise small inhibition of the gastrocnemius as compared to the monosynaptic potential obtained

20 degrees from full flexion. If an effect was obtained at the position of extension it could be small and sometimes absent at the position of flexion but it was, as a rule, never the same as the one at the position of extension.

To sum up: these experiments show that if an effect is obtained, for instance on an extensor, the effect on the flexor is always the opposite. On the other hand, a certain position of the joint does not always give a reflex effect.

The afferent inflow responsible for any effect could in some experiments be sufficiently controlled afterwards. It has only been possible to do that in case of the medial nerve. Successful experiments of this type have not been very many as is but natural. All effect had to be abolished after cutting the joint nerve, then the routes on which the joint fibres reached the cord were investigated and in some cases it was possible to record action potentials on the peripheral stump of the divided joint nerve. In two cases with no effects of electrical stimulation of the medial nerve this derived entirely from the cut obturator nerve. In four cases with no detectable effects of electrical stimulation, the whole medial nerve derived from the saphenous nerve and was connected to active endings both at flexion and extension. In two cases with natural stimulation there was a strong effect at flexion but none at extension. In these cases the medial nerve had two branches and the lower one was derived from the cut obturator nerve and connected to endings active at extension, whereas the upper derived from the saphenous and was connected to endings active at flexion only (compare Chapter II).

In the experiments with natural stimulation the size of the monosynaptic potential from various muscle nerves has been compared at different positions of the tibia relative to the femur. Thus these experiments do not analyse the effects on muscles during the changes of position. As pointed out in Chapter II the sum total of the afferent inflow from the joint receptors during movements must form a very complicated pattern. Furthermore changes of position cannot be investigated by the monosynaptic method. The reason for this is that tests cannot be elicited often enough to catch the effects during movement because of the many

complications following in the wake of rapidly elicited test shocks (LARRABEE and BRONK 1947; LLOYD 1949; BROOKS, DOWNMAN and ECCLES 1950; BROCK, ECCLES and RALL 1951; ECCLES and RALL 1951 a, b). The facts mentioned above make it very difficult to uncover the influence of the joint receptors on the muscles. Last but not least in experiments, such as those reported in which the muscles have to be denervated, the receptors in the joint capsule work deprived of the influence which the muscles normally would exert upon them.

Fig. 28 shows the monosynaptic potential of the biceps-semitendinosus muscle recorded in S 1 when the tibia is at a position of 165 degrees and moved to 180 degrees and back again to 165 degrees. There is seen a facilitation of the biceps-semitendinosus at 180 degrees as compared to the position of the tibia at 165 degrees. In B the same change of position was carried out but at the same time the quadriceps muscle was pulled upon. This time there was no effect on the monosynaptic potential. (In order to show up the effect better, the test shock had been somewhat increased, but the same result was seen with the weaker stimulus used in record A.) In this same experiment the effect on the monosynaptic potential of the quadriceps turned from inhibition to a very small facilitation at 180 degrees as compared with 165 degrees, when the muscle tendon was pulled upon. Pulling on the denervated quadriceps muscle is a rough and artificial way of influencing the joint receptors to alter the effect on the monosynaptic potentials elicited from the muscle nerves. It is not in any way interpreted as being of specific functional importance. But it shows that the tension of the muscles attached to the joint adds something essential to its afferent inflow.

To find out what muscle tension might do to the activation of joint receptors a series of experiments were made, using decerebrate cats only, and leaving intact all nerves except the medial joint nerve, from the distal stump of which action potentials were led off in the way described in Chapter II.

Fig. 29 shows the results from such an experiment where action potentials have been recorded from the undissected medial nerve.

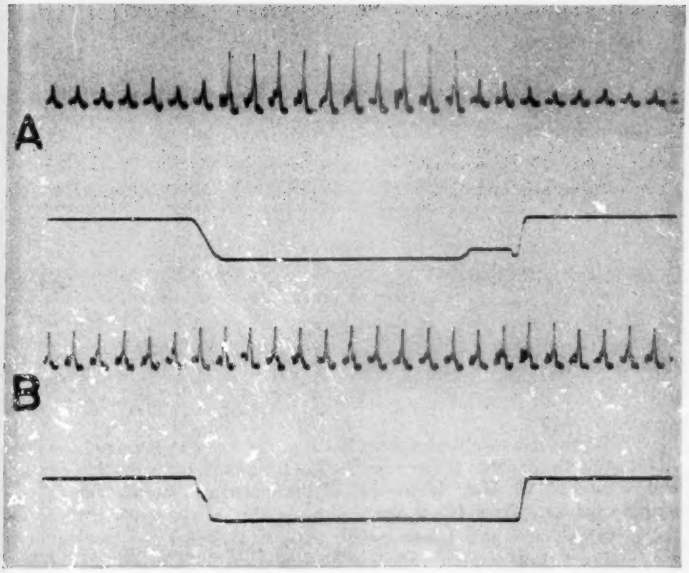

Fig. 28. Spinal cat. Monosynaptic reflex elicited from the biceps-semitendinosus muscle once per second and recorded from the ventral root S1. In A the reflex is facilitated by altering the position of the tibia from 165 degrees to full extension. In B the same movement is made as in A and at the same time the quadriceps muscle is pulled upon. No effect is seen to occur. The stimulation has been increased in B to reveal more clearly the abolition of the effect. A full description is given in the text.

In A the joint is flexed by a forced movement against the contracting quadriceps muscle. A tremendous discharge is seen which suddenly decreases as the muscle gives away in response to the increasing tension (the lengthening reaction of SHERRINGTON 1909). In B the same movement of the tibia is repeated while the skin over the heel is intensively pinched. HAGBARTH (1952) showed that such a stimulus is a potent inhibitor of the quadriceps muscle. As is seen the discharge in the joint nerve decreases and fewer endings are activated. In C the same movement is repeated after section of the quadriceps nerve. In this record the discharge has decreased even more. (The speed of the movement in the

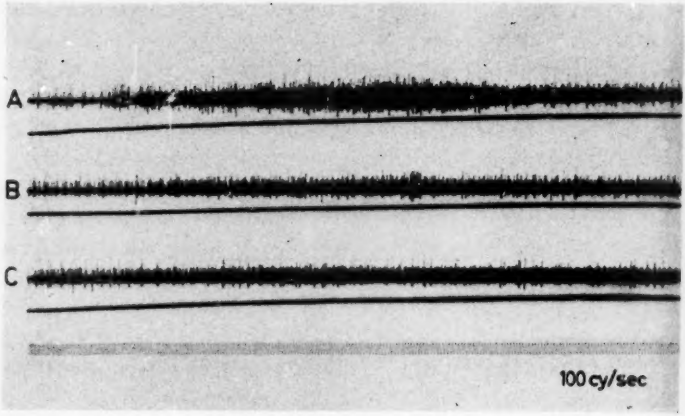

Fig. 29. Decerebrate cat. The response in the medial nerve to flexion of the knee. A. Intact nerve supply to the muscles. B. The same as A, while the skin over the heel is pinched. C. After denervation of the quadriceps muscle. For full description see text. Time: 100 cy/sec.

different records seems from the signal line not to be strictly comparable, but the amplification of the movement is very high and the movement, only a few degrees in range, is as seen very slow.) It was not possible to produce such great effects, as seen in Fig. 29, in all animals. When the effects were small, very few active endings were represented in the medial nerve as revealed by pressure on the capsule with a glass rod.

Fig. 30 shows an experiment where after dissection of the medial nerve three spikes were left. In A is seen the response of the three sensory endings, one firing at high frequency and the other two at low frequency. The joint has been forced to a fixed position against the contraction of the quadriceps muscle, and the sensory endings have been allowed to adapt themselves. In B the nerve to the quadriceps muscle has been cut. In spite of this, two of the sensory endings fire with the same frequency as before, but the third has lowered its frequency to half the value of the upper record. Cutting the medial collateral ligament silenced one of the spikes which were unaffected by the dener-

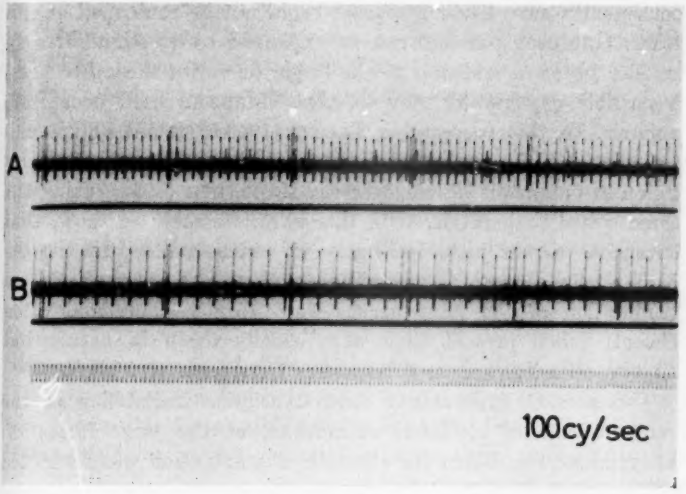

Fig. 30. Decerebrate cat. A. The response of three sensory endings connected to the medial nerve at a position of a few degrees flexion. The nerve supply to the muscles is intact. B. The response of the three sensory endings at the same position of the tibia after cutting the quadriceps nerve. (Amplification is increased somewhat in B to secure the response after denervation.) Time: 100 cy/sec.

vation of the quadriceps. It could be brought into action again by loading the ligament. The origin of the other two spikes could not be located with certainty; but it seemed that the one affected by cutting the muscle nerve lay in the region of the medial patellar ligament.

This experiment shows that an increase of muscle tension at a fixed position of the joint can increase the frequency of some active sensory endings. The joint receptors thus signal resistance to movement both by an increase of the impulse frequency and an increase of the number of active endings.

DISCUSSION

The finding of GARDNER (1950) that in the decapitate animal stimulation of the large fibres in the nerves to the knee joint

consistently gave flexor responses could not be confirmed in this work. GARDNER's results can be explained by co-stimulation of smaller fibres in addition to the larger ones. On the other hand a possible explanation may be that GARDNER used decapitate animals. In this preparation LLOYD (1943 b) found only facilitation of the flexors and inhibition of the extensors on stimulation of cutaneous nerves, whereas HAGBARTH (1952), using the same spinal preparation as in this work, was able to show, that cutaneous nerves yield facilitation of extensors too. In the decerebrate preparation, according to GARDNER, the effects on stimulation of the joint nerves were very variable and often absent. When present they were usually flexor in nature but on two occasions extensor responses were seen.

The present experiments showed a great variability of the reflex effects of electrical stimulation of the large fibres of articular nerves. When the strength of stimulation was restricted to just above threshold for the large nerve fibres, the responses were small or absent and when present as often facilitation as inhibition of either extensors or flexors. However the effects were always reciprocal. This was, on the basis of the experiments where the afferent inflow was controlled, interpreted as follows. The endings active at extension are not the same as those at flexion (Chapter II) and they may have different effects. A simultaneous stimulation of all the fibres will then, if they are evenly distributed to endings active at flexion and at extension, give no or undetectable effects on the monosynaptic mass test (see GRANIT and STRÖM 1951). Sometimes one of the components is better represented than the other, and a small effect will result. The great variation of fibres in the joint nerves, as shown in Chapter I, and the severance of the obturator nerve is the explanation f the variations in the afferent inflow from the joint.

The interpretation presented above of the variability of the effects on electrical stimulation of the joint nerves is supported by the findings on natural stimulation of the joint receptors. This was found to produce reciprocal effects on extensors and flexors of the joint. On the other hand the effects varied greatly

in size from animal to animal. They were often small and sometimes absent. This can also be explained by the variation of fibres in the joint nerve and the severance of the obturator nerve, which may contain all or a large component of the fibres in the medial nerve.

From the experiments on the reflex effects of stimulation of joint nerves no conclusions can be drawn with regard to the action of the joint receptors on the muscles in locomotion. No curves of the time courses of the effects of electrical stimulation are given because they would throw no light upon the mechanisms of locomotion. Such effects can to some extent be elucidated by testing the monosynaptic reflex at different positions of the joint during movements of different speeds and afterwards studying the afferent inflow from the joint to see what impulse patterns are responsible for possible effects. Both the total afferent inflow from the joint as well as impulses from single endings have to be used as conditioning stimuli and tested on single motoneurones to uncover all the effects on the muscles which are mixed up in the complicated afferent inflow from the joint. (These problems will also be treated in the General Discussion.)

The experiments presented here of the effects of the joint receptors on the muscles lend support to the finding in Chapter II that there are different endings working at different positions. If not, one would expect the same effects on one and the same muscle to happen when setting the tibia either at extension or flexion. This was not found to be the case.

The results of the experiments with decerebrate cats, where the sensory discharge from the knee joint was shown to be related to the tension of the quadriceps muscle, must mean that the joint receptors signal resistance to movement. It is most likely from the results presented here and in Chapter II that the endings responsible for this discharge lie in the capsule or in the medial patellar ligament. No evidence presented here excludes the idea, that these endings could at the same time be recorders of position, but their status as resistance recorders is established.

The reflex effects studied here have shown, that the joint

receptors recording position, movement and resistance to movement in a limb at the same time are involved in the control of these things. On the other hand to find out what this control is and the rules for it deserves further experimentation.

SUMMARY

1. The reflex effects of stimulation of knee joint nerves on flexors and extensors of this same joint have been investigated in decerebrate and low spinal cats. The effect of muscle tension on some of the joint receptors has been investigated in decerebrate cats.

2. The reflex effects of electrical stimulation of the large articular nerve fibres were found to be very variable in different animals, giving sometimes inhibition and sometimes facilitation of flexors and the reciprocal effect on extensors. These effects were small and sometimes absent, but when present always reciprocal on the flexors and extensors of the joint.

3. Adequate stimulation of the endings connected to the medial nerve also gave variable effects which were also always reciprocal.

4. The great variability of joint reflexes on muscles is explained as being due to a combination of the mass test used (the monosynaptic potential from a whole ventral root) and the great variability in the nerve supply to the knee joint. The conclusion is drawn that these experiments lend support to the findings in Chapter II, that different endings are active at flexion and extension.

5. In decerebrate animals an increase in tension of the quadriceps muscle increases the number of joint receptors active at a certain position and the impulse frequency of some of those already discharging at that position. From these experiments the conclusion is drawn that some of the joint receptors are able to signal resistance to movement.

6. The reflex effects obtained show that the joint receptors recording position, movement and resistance to movement already at the spinal level are involved in the control of these things.

CHAPTER V

Projections of afferent fibres from the knee joint to the cerebral cortex

If the signals of joint receptors discriminating position, movement and resistance to movement of a limb are perceived, they are likely to be represented in the sensory areas of the cerebral cortex. The technique making use of evoked potentials (GERARD, MARSHALL and SAUL 1936; MARSHALL, WOOLSEY and BARD 1937; ADRIAN 1940, 1941, 1943; MARSHALL, WOOLSEY and BARD 1941; WOOLSEY 1947) is now an established method to find out the cortical representation of different afferent systems.

GARDNER and NOER (1952) and GARDNER and HADDAD (1953) stimulated the posterior nerve and recorded evoked potentials in the sensory cortex. They did not, however, determine which fibres were stimulated, nor did they give the latencies for the evoked potentials. From the pictures published in the paper by GARDNER and NOER one finds the latency of an evoked potential from the posterior joint nerve to be 18—20 milliseconds. MOUNTCASTLE, COVIAN and HARRISON (1952) stimulated various structures other than muscles and skin, amongst which also were joints, by a mechanical device, and found that the impulses set up by such a stimulus reached the cortex in the same time as impulses from the skin in the same region of the limb. These authors also state, that the latency for Group III fibres of the muscle nerves is twice that for the fibres of Group II and the latency for these from the hind limb in the region of the knee was given as 10 milliseconds. The latency of the evoked poten-

tials in the work of GARDNER and NOER points to Group III fibres as the afferent channel. According to the present investigation (Chapter I and II) Group III fibres do not mediate the impulses signalling position, movement and resistance to movement. Thus the papers by GARDNER et al. do not show whether impulses from joint sensory endings signalling position and movement reach the cerebral cortex. MOUNTCASTLE et al. do not define which nerves were left in connection with joints in their "isolated limb", and used mechanical stimuli which could have activated endings lying in structures other than joints.

METHODS

Successful records of evoked potentials from the articular nerves were obtained in 21 cats. Of these only five were used for experiments on the posterior nerve. The animals were anaesthetized with either nembutal alone, 20—30 mg/kg body weight, or 15—20 mg chloralose/kg body weight. The anaesthetics were given intraperitoneally. The skull was opened with a wide craniectomy over both hemispheres. Either the medial or the posterior knee joint nerve was dissected free. The brain surface and the nerves were kept moist with warm paraffin oil.

The articular nerves were stimulated with square waves of less than 0.5 milliseconds' duration. The threshold stimulus and spread of current were controlled in the way described in Chapter IV.

Evoked potentials were led off from the pial surface of the brain with a silver wire electrode isolated to its tip which was formed to a ball. The indifferent electrode was always in the frontal sinus. Evoked potentials were recorded with positivity upwards on the oscilloscope by the recording system described in Chapter II.

In two cats out of five section of the dorsal funiculi of the spinal cord was performed successfully, that is to say the animals recovered very soon from spinal shock and had normal blood

pressure. The sections were controlled histologically on frozen sections of the cord.

The terms ipsilateral and contralateral are used with reference to the joint nerves.

RESULTS

The level of anaesthesia is all important for the recording of evoked potentials elicited from the articular nerves. In the animals anaesthetized with nembutal alone it was often necessary to wait several hours for optimal recording conditions. Substituting some of the nembutal with chloralose made it possible to record the evoked potentials almost immediately after the operation.

The procedure in each experiment was as follows. First either the saphenous or the sural nerve was stimulated and the point of maximal response in sensory areas I and II (WOOLSEY 1947) searched for. When the potential from the skin nerve was quite constant, evoked by every stimulus and with a constant latency of 10—12 milliseconds, stimulation of the joint nerve was started. To begin with the threshold stimulus was determined, and the

Fig. 31. Sites of response (indicated by dot) in sensory areas I and II to stimulation of the medial nerve shown on standard drawing of the cat's brain.

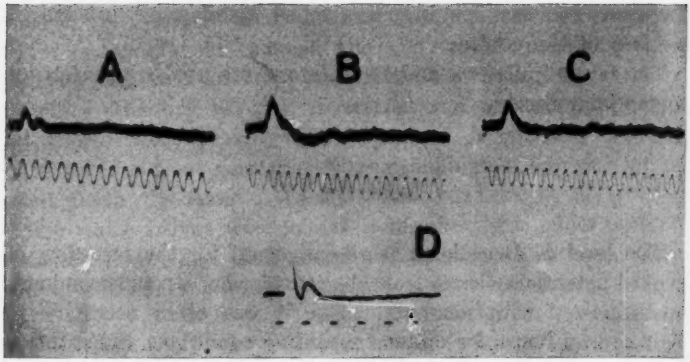

Fig. 32. Responses in the sensory areas of the cortex to stimulation of the medial nerve (shock artefact indicated by dot). A, contralateral sensory area I. B, contralateral area II. C, ipsilateral area II. Time: 100 cy/sec. D, threshold stimulus to the medial nerve. Time: 1 000 cy/sec.

stimulus set just above threshold. At this stimulus strength spread of current was controlled; this was found to be easiest in the case of the medial nerve. When the stimulus had been adjusted in this way evoked potentials in the cortex were searched for.

Just lateral to the point of maximal response for the cutaneous nerves in both contralateral sensory areas I and II, and in the ipsilateral sensory area II (see Fig. 31), initially surface positive potentials, sometimes followed by a negativity of lower amplitude and longer duration, could be detected on stimulation of the joint nerves. Fig. 32 shows the response in these three receiving areas on stimulation of the medial nerve. In the contralateral sensory area I it was often more difficult to find an evoked potential because it was masked by background activity. In the records of Fig. 32 it can be seen that the latencies for these responses are 10—15 milliseconds, being shortest in the contralateral sensory area I. The evoked potential lasts about 20 milliseconds. The latency of the response varies with the depth of anaesthesia. Increasing the stimulus strength increases the response and sometimes makes it diphasic. Fig. 33 shows the response from contralateral sensory area I with a stimulus just above threshold

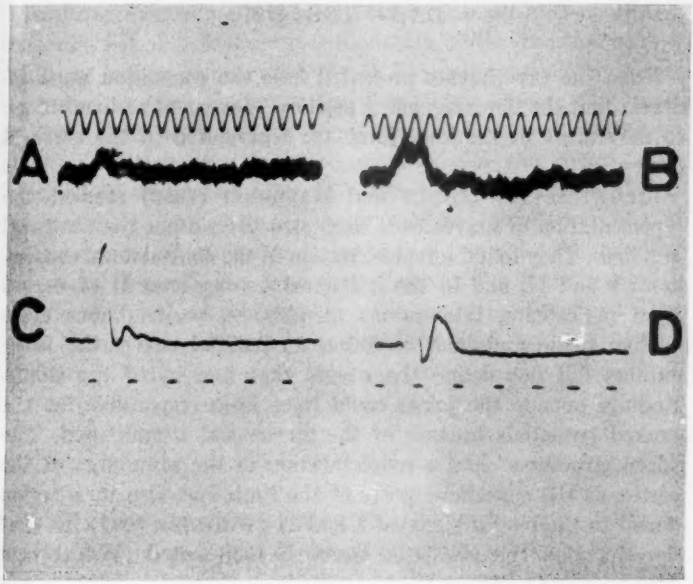

Fig. 33. A shows the response in contralateral sensory area I to threshold stimulation of the medial nerve (C). B shows the response in the cortex to an increased stimulus to the medial nerve (D). Time: 100 cy/sec in A and B and 1 000 cy/sec in C and D.

on the joint nerve (A). In B the stimulus has been increased and the cortical response has also increased and become diphasic.

In the two animals in which the dorsal funiculi were cut successfully it was not possible with a slightly superthreshold stimulus to get any cortical response.

In the cats anaesthetized with chloralose in addition to nembutal a response in the ipsilateral sensory area I was sometimes obtained. There was always a difference in latency between the response in the contralateral and ipsilateral areas, the ipsilateral one having a longer latency. The response in the ipsilateral sensory area I was more easily obtained the heavier the chloralose dosage. The pathways for this response were not systematically explored.

DISCUSSION

From the experiments presented here the conclusion must be drawn that the fibres signalling position, movement and resistance to movement in the knee joint are represented in the cerebral cortex.

MOUNTCASTLE, COVIAN and HARRISON (1952) studied the representation of nerves from deep structures other than muscles in a limb. They found a representation in the contralateral sensory areas I and II, and in the ipsilateral sensory area II of nerves from periosteum, interosseous membranes, peritendinous connective tissue and joint capsules. As pointed out earlier these authors did not define the nerves that innervated the joints. Endings outside the joints could have been responsible for the evoked potentials because of the mechanical stimuli used. The "deep structures" had a representation in the same area of the cortex as the superficial parts of the limb, but also in a region dorsal to the ones designated I and II (WOOLSEY 1947). In that dorsal region the vestibular nerve is represented (WALZL and MOUNTCASTLE 1949). Evoked potentials from the joint nerves were searched for in this region but never obtained. On stimulation of the "deep structures" of the forelimb MOUNTCASTLE et al. (1952) found a cortical latency of 7—8 milliseconds which is equal to the latency for the skin receptors in the same region of the limb.

In the present investigation the latencies for the evoked potentials varied with the depth of the anaesthesia, but in optimal recording conditions they were about the same as those of cutaneous nerves, that is to say, around 10—15 milliseconds. This is to be expected because the joint nerves have the same calibre spectrum as cutaneous nerves. MOUNTCASTLE et al. (1952) showed that impulses from the Group II fibres in the mixed tibial nerve reached the cerebrum in 10—12 milliseconds and the Group III fibres in 18—20 milliseconds. A latency of 20 milliseconds of the cortical response of articular fibres in the work of GARDNER and NOER is probably best explained as merely an effect of too deep anaesthesia.

In the experiments in which incisions were made in the posterior funiculi, evoked potentials to stimulation of the articular nerves could no longer be recorded. There is some evidence from the work of GARDNER, LATIMER and STILLWELL (1949), that large articular fibres ascend in the dorsal funiculi. GARDNER and NOER (1950) say, that they recorded potentials in the cortex after incisions in the dorsal funiculi. GARDNER and HADDAD (1953) found evoked potentials in the cortex on stimulation of the posterior nerve after various incisions in the spinal cord including the dorsal funiculi. No latencies are given for these responses nor did they control the stimulus with regard to stimulated fibre sizes. Hence it is difficult to accept their work without further evidence.

SUMMARY

1. The cortical representation of the medial and posterior nerves from the knee joint of the cat were studied while restricting the stimulation to fibres connected to the sensory endings, which signal position, movement and resistance to movement.

2. Both medial and posterior nerves were found to be represented in the contralateral sensory areas I and II and in the ipsilateral sensory area II. The latencies for these responses were with optimal recording conditions 10—15 milliseconds and the evoked potential lasted about 20 milliseconds.

General Discussion

MOUNTCASTLE et al. (1952) and MCINTYRE (1953) showed that there is no direct representation of the Group I fibres of muscle nerves in the cerebral cortex. Contrary to MOUNTCASTLE et al. the latter author found a direct representation in the cerebral cortex of the Group II fibres of muscle nerves. "These statements", to cite GRANIT (1955), "are subject to the limitations of the technique of evoked potentials and raise the question of whether a representation might not be found if one knew what systems it would be necessary to facilitate in order to make the technique more sensitive".

In Chapter I it is concluded that an unknown number of articular fibres taking their way through the muscles will add to the Group II fibres of muscle nerves. This is important in relation to the finding of MCINTYRE, that a representation of Group II fibres in the muscle nerve exists in the sensory areas of the cortex. Further experimentation is required to settle this and many other questions with regard to what proportion of Group II responses might be articular rather than muscular. It will be necessary to investigate various muscle afferents from this point of view. At present, however, it is impossible to say if the afferent fibres from muscles do contribute to the fibre system mediating information of position, of passive and active movement and of resistance to movement to the cerebral cortex, but from the results presented in this work it can at any rate be stated that the joint receptors providing such information actually have the cortical representation one would expect as part of a cortical control

As pointed out in Chapter I the nerve supply of the joint from direct articular nerves and through muscles varies from animal to animal. Furthermore, the two nerves running directly to the same joint have to be studied separately. However, the

posterior nerve can only be studied over part of the range from flexion to extension. These factors restrict the analysis of the total picture of the sensory message from the joint as does also the technique for recording action potentials, because in one and the same nerve only one or a few endings can be analysed in detail.

The varying knee joint innervation introduces difficulties not only when studying the afferent inflow from the joint. It also makes it difficult to work out the way in which the joint endings function in processes of locomotion; the more so as the joint nerves through the muscles cannot be studied separately from the muscle nerves.

According to GARDNER (1944) there are many articular fibres reaching the knee joint via the quadriceps muscle. These will add both to Group I and II fibres of the muscle nerve. Those adding to Group I fall mainly in the 12—15 microns group (see calibre spectra in Chapter I). It thus seems that the smaller Group I fibres will be relatively more numerous in the quadriceps nerve compared to muscle nerves which lack articular fibres. This is interesting because in the nerves to the thigh muscles Group I can be separated in two subgroups (BROCK, ECCLES and RALL 1951; BROCK, COOMBS and ECCLES 1952; BRADLEY and ECCLES 1953). We are lacking knowledge about articular branches, within the nerves of the biceps and the semitendinosus. At any rate, the addition of articular fibres in the lower range of Group I fibre sizes might be of importance for the experimental subdivision of Group I in the nerve to the quadriceps muscle.

The findings in Chapter IV that the joint receptors measure the tension of the quadriceps muscle are interesting also from the point of view of their effect on the alpha motoneurones (GRANIT 1955). There is thus a nervous loop outside the muscle measuring its tension and at the same time conditioning tension. One of the endings described in Chapter IV influenced by muscle tension, seemed to lie in the neighbourhood of the medial patellar ligament which is closely associated with the quadriceps muscle. The arrangement in which a joint measures the tension of a muscle attached to it is of course specialized. We lack detailed

knowledge about the innervation of tendons, which in this connection is of great interest. But WRETE (1956) has found that the Achilles tendon in man gets part of its innervation from branches of the sural and tibial nerves. It might be a general rule that muscle tendons get part of their innervation from nerves running outside the muscles.

That joint receptors recording muscle tension influence the alpha motoneurones could be settled, but it would be more difficult to find out if they at the same time influence the gamma motoneurones. The muscle must be denervated, if impulses from the joint receptors activated by the muscle are not to be confused with impulses from muscle endings. The influence on the gamma motoneurones would therefore have to be studied in the central stump of the muscle nerve, which has been found difficult on account of the very variable background activity in the gamma motoneurone pool of a totally deafferented limb. If the muscle tendon is freed from its attachment to the joint, and the impulses from a muscle spindle are recorded in a dorsal root filament while the joint is manipulated, any possible effects through the gamma efferents on the spindle might be set up by endings in the joint which do not measure the muscle tension.

ELDRED and HAGBARTH (1954) in studying skin reflexes found that an effect on the alpha motoneurones is always accompanied and in fact preceded by a similar one on the gamma motoneurones. It is possible that receptors measuring tension of a muscle also have effects on the gamma motoneurones. This is an important question because there is no excitatory proprioceptive reflex from the muscle spindle on the gamma motoneurones (HUNT, 1951). A loop outside the muscle nerve measuring the muscle tension might by working on the gamma motoneurones indirectly fulfil that function. This problem might be solved by a further knowledge of the anatomy and function of that part of the innervation of tendons taking its course outside the muscle.

The representation in the sensory cortex of the large joint fibres means that information about position, active and passive movement and of resistance to movement has a chance of being perceived. The joint receptors also discriminate speed and di-

rection of movement. This might mean that the cortex gets indirect information about which muscles (extensors or flexors) are active and the speed of their contraction.

The findings of this work on knee joint innervation in the cat can of course not be applied directly to man. Nevertheless it is of some interest to dicuss in this connection, briefly at least, some of our knowledge of the "muscle sense" in man.

The nerve supply to various joints in man shows a wide variation (RÜDINGER 1857). WRETE (1949) in an investigation of the innervation of the shoulder joint in man describes variations in its nerve supply, and he also clearly states that there are branches running to the joint via the muscles. There are, according to WRETE, both autonomic and sensory components in these articular branches. The types of sensory endings found in the knee joint of man are the same as those found in the cat (KELLGREN and SAMUEL 1950). It thus seems that there are many similarities in the innervation of joints in animals and man.

In a classical study GOLDSCHEIDER (1889) investigated "muscle sense" and attributed most of the sensations involved to joints. With the technique he used all sorts of endings in the limb were activated, but he was able by means of faradization of the joints to abolish some of the effects.

GOLDSCHEIDER stated that minute changes of joint position of less than one angular degree is perceived as a movement and not as a set of successive positions. He further stated, that for passive movements the minimal perceptible excursion in the knee joint is 0.5—0.7 degrees if the speed reaches 1—2.5 degrees/sec. The limen for perception of willed movements is slightly lower. GOLDSCHEIDER also found that a movement too slow to be felt, if of small excursion, becomes perceptible if it is prolonged.

Such small angular deviations as studied by GOLDSCHEIDER have not been investigated in the knee joint of the cat, but it follows from the results reported that the functionally overlapping sensory endings may very well signal small variations in position as movement. With the existing arrangement of the endings

it is quite easy to understand that slow movement can be perceived provided it has a certain amplitude.

SHERRINGTON (1900) stated, that there is only a slight impairment of the muscle sense if the skin is anaesthetized, but very great disturbances are set up by injury to deeper structures. MEYER (1921) claimed that anaesthetizing the skin over the elbow joint markedly increases the threshold for detection of passive movement. Such an anaesthesia might quite well abolish some of the innervation of the joint too (RÜDINGER 1857).

In 1921 STOPFORD studied the innervation of the interphalangeal joints in patients with lesions of cutaneous nerves in the hand which give branches to the joint (RÜDINGER 1857). He reported that such patients can feel passive movements but the impression of direction, degree and site of movement is greatly impaired. His findings are not in accordance with the statements of HEAD et al. (1905 a and b) who claimed that the fibres subserving deep sensibility run mainly with the motor nerves and must pass to such deep structures as joints along tendons and possibly along blood vessels. But WRETE (1956) in a preliminary investigation has not found any nerves running along or directed to the tendons of the muscles in the forearm which insert in the hand. STOPFORD did not investigate the ability of his patients to appreciate resistance to movement. It would be of interest to know if the sensation of resistance was appreciated by these patients. If it had been so, the sensation might have arisen in the sensory endings of the periosteum where most muscles have their insertion. Impulses from these endings have been shown by MOUNTCASTLE et al. (1951) to reach the sensory cortex with the same latency as impulses from the cutaneous endings in the same region. The fibres must then be of Group II sizes and possibly some of them run via muscles and are then added as joint fibres to the Group II fibres of the muscle nerves.

LAIDLAW and HAMILTON (1937) studied the appreciation of movement and found that the determination of the direction of a movement must be a separate factor; movement is recognized before one can determine its direction. In the light of the findings in the knee joint of the cat the explanation may be that the move-

ment has to reach a certain range before one single ending can tell the direction of a movement. Several endings overlapping may then decrease the range of movement needed for appreciation of the direction, and more the more numerous they are.

It is well-known that diseases involving the dorsal funiculi lead to impairment of deep sensibility and loss of position sense. In this connection it may be noted that the present investigation showed that the cortical evoked potentials of the large articular fibres were abolished on cutting the dorsal funiculi.

The parallels drawn above between clinical findings in man and experimental results in the cat are of course not decisive. However, all facts point in the same direction, namely that nerve fibres from joints contribute largely to the fibre system mediating the various sensations involved in "muscle sense".

General Summary

This is an anatomical and physiological investigation of the innervation of the knee joint in the cat. Its aim is to elucidate the spike pattern from joint nerves in relation to a variety of stimuli involving position, movement and resistance to movement in a limb and the contribution of muscular forces acting on the joint capsule. Such spike patterns are involved in the so-called muscle sense.

The first chapter deals with the distribution, termination and calibre spectra of the knee joint nerves. The joint receives its innervation partly from direct articular nerves, the medial and the posterior one, and partly from nerves running via muscles. The relative contributions from one or the other of these routes are very variable from animal to animal, as is reflected also in the varying number of fibres found in the direct articular nerves.

The two direct articular nerves have a calibre spectrum which resembles that of a cutaneous nerve. The fibres of the 10—15 microns group innervate Golgi endings which are found only on the ligaments of the joint. This group of fibres also supplies modified Vater-Pacini corpuscles of which there are very few in the joint capsule. In the capsule lie also Ruffini-like endings which are connected to fibres of the 7—10 microns group. It is pointed out that joint afferents through muscles will add an unknown number of fibres to the Group I and II of some muscle nerves.

In Chapter II the physiological response of the sensory endings of the joint is analysed. Most of the sensory endings connected to the medial nerve are active at a joint position of full flexion or full extension. In the posterior nerve more endings are active at full extension than in the mid-position between flexion and extension. Variations in the pattern described above have been ascribed to the variability of the nerve supply to the joint. The

Golgi endings and the Ruffini endings are slowly adapting and the modified Vater-Pacini corpuscles rapidly adapting. By means of their impulse frequency the endings signal the position, direction and speed of active and passive movement of the joint.

The responses are divided into three types which are associated with the different types of endings. Thus type 1 is the slowly adapting discharge from the Golgi organs which are not influenced by the muscles attached to the joint, because they lie in the medial collateral ligament and the cruciate ligaments. This type of receptor records the exact position of the joint and the direction of a movement of the joint. It is, however, rather insensitive to movement and is thus hardly capable of measuring its speed. The type 2 is the Ruffini ending which, since it lies in the capsule itself, works under the influence of the muscles attached to it. This receptor records movement but is not, owing to its greater sensitivity to movement as compared to type 1, suited for recording the exact position of the joint. The type 3 response derives from the modified Vater-Pacini corpuscle which is very sensitive to quick movement and vibration and may serve as an acceleration receptor.

In Chapter III the dorsal root distribution of the fibres in the posterior and medial nerve is investigated. The medial nerve enters the spinal cord via the 5th and sometimes the 6th lumbar dorsal root, the posterior nerve via the 7th lumbar and sometimes the 1st sacral dorsal root. The fibres of the medial nerve reach the joint via the saphenous and/or the obturator nerve. The conduction rates of the articular nerve fibres are in good agreement with their calibre spectrum. Stimulation of ventral roots showed no contribution of somatic efferent fibres to the joint nerves.

In Chapter IV some of the interrelations of the knee joint receptors and the flexors and extensors of the same joint are investigated in decerebrate and low spinal animals. Both electrical and adequate stimulation of the articular nerve fibres were used as a conditioning stimulus. The effect on the monosynaptic potential of flexors and extensors is very variable, usually small and often absent but when present always reciprocal. This varia-

bility of the effect is explained as being due to a combination of the mass test used (the monosynaptic potential recorded on a whole ventral root) and the variability of the nerve supply to the joint. These experiments support the conclusion that there are different endings working at different positions of the joint. The reflex effects from the joint could be altered if the quadriceps muscle was pulled upon because this also alters the afferent inflow from the receptors in the joint. In decerebrate cats it could be shown that some of the joint receptors signal the tension of the muscles and thus resistance to movement. The reflex effects show that the joint receptors recording position, movement and resistance to movement already at the spinal level are involved in the control of these things.

In Chapter V the cortical representation of the large articular fibres was investigated. The fibres signalling position, active and passive movement and resistance to movement have a direct representation in the contralateral sensory areas I and II and the ipsilateral area II. Their impulses reach the cortex with a latency of 10—15 milliseconds which is the same as for a cutaneous nerve from the same region.

In the General Discussion a comparison is made between the findings in the knee joint of the cat and a number of facts about "muscle sense" in man. There are many similarities which make it highly probable that impulses arising in joints are important and play a major role in the sensations of "muscle sense".

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